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THE PROBLEM OF SPECIES IN OENOTHERA[1]

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IT is altogether fitting that the seventy-fifth anniversary of the founding of the oldest biological journal in the United States should be celebrated by the country's oldest general biological society. It is not merely similarity in age, however, that makes this a fitting celebration: it is rather the fact that THE AMERICAN NATURALIST and the American Society of Naturalists, although independent in origin, and at no time in their long history organically connected, have had common interests and ideals and have tended to emphasize the same aspects of the broad field of biology. The society and the journal have both been characterized by breadth of viewpoint and by an emphasis upon those aspects of biology which are the common concern of all students of the life sciences, whether they be botanists or zoologists. They have thus served as a unifying influence during a period when the biological fraternity has tended to break up into a multitude of isolated and often mutually exclusive groups. The society takes this opportunity to felicitate the journal, therefore, upon seventy-five years of brilliant service

[1] Presidential Address, American Society of Naturalists, December, 1942. The program of this meeting was planned in celebration of the seventy-fifth anniversary of THE AMERICAN NATURALIST. The meeting, which was to have been held in New York City, was cancelled at the last moment at the request of the Office of Defense Transportation. The work reported in the paper has been supported in its earlier stages by the Penrose Fund of the American Philosophical Society and in recent years by the Rockefeller Foundation.

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to the whole of biology, and to congratulate it upon the high level of excellence which its pages have maintained, and upon the influence which it has exerted upon the development of biology and the unification of biologists. It extends its best wishes for a long and equally brilliant career in the future. It is happy that it now shares in the responsibility for maintaining the high excellence of the journal through a board of advisory editors chosen by the society. It is to be hoped that the journal and the society will cooperate for many years to come in the furtherance of those aims and ideals which all biologists hold in common.

In view of the predominant interest of both THE AMERICAN NATURALIST and the American Society of Naturalists in the study of organic evolution, it seems appropriate that I should select a subject dealing with this general field of study. I have, accordingly, chosen to speak upon "The Problem of Species in *Oenothera*."

The genus *Oenothera* is a large and varied assemblage, which ranges widely over the Western Hemisphere. If we adopt the classification of Munz (1928–1938), it includes fifteen subgenera. All these are found in North America, ten of the fifteen being confined to this continent. Five subgenera (*Sphaerostigma, Lavauxia, Hartmannia, Raimannia* and *Euoenothera*[2]) extend down into South America, some forms reaching the southern extremity of Argentina and Chile. Of the subgenera confined to North America, six are restricted almost wholly to regions west of the Mississippi River, being especially abundant west of the Rockies. Only four subgenera (*Calylophis, Raimannia, Kneiffia* and *Euoenothera*) reach the eastern states. Very little is known in regard to the cytogenetics and the phylogenetics of most of these subgenera. Schwemmle and his students (1927–1939) have done some work on *Raimannia* and *Hartmannia*, and a few minor cytological observations have been made on

[2] Dr. Munz informs me that the term *Onagra* should be supplanted by the term *Euoenothera*. I am consequently using the latter term in this paper.

other subgenera. With these few exceptions, however, all the extensive cytogenetic work on *Oenothera* has been confined to the North American forms of the subgenus *Euoenothera* and to certain European races of this subgenus which have been introduced into that continent from North American sources. The situation which has been found to exist in this subgenus, however, is so unusual that it is highly desirable that the other subgenera be investigated also with comparable thoroughness. A beginning is being made in this direction at the present time, the results of which will be mentioned later.

It is not my purpose to discuss in detail at this time the peculiarities of the cytogenetic behavior of *Euoenothera*. These are already well known to most biologists. I wish rather to show how these peculiarities have led to an unusual taxonomic situation and how it has been possible to acquire an understanding of the essentials of this situation as a result of cytogenetic analyses. I will deal first with the North American euoenotheras, and later will briefly compare the situation found in this group with that found in the South American members of this subgenus and other subgenera.

Taking up the North American euoenotheras, then, it is first necessary to emphasize the fact that those found in California, Northern Mexico and contiguous areas differ in their cytogenetic behavior from those which grow farther east and north, in that they do not show in any marked degree the peculiarities which characterize the North American euoenotheras as a whole. They have for the most part paired chromosomes in meiosis and they lack lethals. The taxonomic problems raised by these plants are not, therefore, in essence different from those raised by other groups with "normal" cytogenetic behavior.

As one proceeds eastward, however, the cytogenetic behavior of the group gradually changes. In the races found in Arizona, New Mexico and Utah, for instance, the chromosomes show a considerable tendency toward

circle-formation, so that a large proportion of a given population, or all of it, will show circles of intermediate size in meiosis. Such configurations as ⊙ 6,[3] or ⊙ 8, or ⊙ 10, or ⊙ 4, ⊙ 6 have been found in most of the plants studied. In a few cases, the chromosomes in these circles seem to have acquired lethals, so that lethal systems, either balanced or unbalanced, have been set up. In other cases, no evidence of lethals has been obtained, and the plants do not breed true to the presence of circles, throwing in each generation a proportion of plants with wholly paired chromosomes, or with only one circle instead of two.

As we proceed still farther eastward and reach the Rocky Mountain region of Colorado, or as we go northward into Washington, we find that practically all plants have a circle of 14 chromosomes in meiosis. This circle carries, almost without exception, a balanced lethal mechanism, so that the plant, which is generally self-pollinating, breeds true for the circle. More than 120 races from the Rocky Mountains and from those parts of the United States and Canada which lie eastward from this region have been examined cytologically by the present author and all but six of these have shown a circle of 14 chromosomes in meiosis, and balanced lethals. It is this great assemblage of circle-bearing and lethal-bearing races which constitutes a taxonomic puzzle which has hitherto defied the efforts of those who have tried to classify them.

That the taxonomic situation within this assemblage is indeed puzzling soon becomes apparent to any one who attempts to study it. All students of *Euoenothera* recognize that multitudinous forms and races exist within the subgenus, but when one attempts to place them in separate categories which might reasonably be called species, one finds himself in difficulties. Thus, Dr. Charles C. Deam, one of our ablest taxonomists, remarks in his "Flora of Indiana" (p. 705): "The plants are exceedingly variable and only an expert can name them

[3] The symbol ⊙ means "circle of."

with any degree of certainty. I have a large number of specimens which I am not including in this treatment because I cannot satisfactorily name them." The result of this situation is that the taxonomists have had to classify the group in a manner which they themselves regard as highly unsatisfactory. Thus, in Gray's Manual we find only five species and one escape recognized which would belong to *Euoenothera*. In Deam's "Flora of Indiana," four species are listed which belong in this subgenus. And yet all taxonomists realize that the situation is not as simple as this—that the small number of species recognized does not take into account the enormous variety which exists in the subgenus. It is the best that can be done, however, with purely taxonomic methods.

The difficulties which confront the taxonomic student of this group owe their existence to certain peculiarities of behavior which will now be explained under four headings.

(1) The euoenotheras which range from the Rockies eastward exist in the form of numerous locally distributed geographical races, which, because of their self-pollinating habit, are more or less effectively isolated from one another. It is because of the presence of these races in such large numbers and the fact that they differ from each other oftentimes in but minor characteristics that the heterogeneity so disconcerting to the taxonomist is introduced into the population as a whole. This heterogeneity is due to a multiplicity of races, and not to variation within the individual races. Each race is made up of self-pollinating individuals, and the race breeds true to a degree rarely attained elsewhere in nature. It is not too much to say that the progeny of a given plant are ordinarily identical with this plant from the genetic point of view. This lack of variability within a race, which contrasts so strikingly with the variability found in the population as a whole, is not a result of homozygosity, for these plants are far from being homozygous—they are often notably heterozygous. It is due rather to the pres-

ence of a circle of 14 chromosomes in which balanced lethals are present. The separation of adjacent chromosomes in the circle into different germ cells produces but two kinds of gametes, genetically speaking, which are identical with those contributed originally to the plant through sperm and egg. The lethals compel recombination of these in selfed line and hence produce plants identical with their parents, except for the results of whatever crossing-over may occur between associated complexes. Crossing-over is apparently a factor of minor significance in *Euoenothera,* however, being probably confined for the most part to the pairing ends, and its occurrence does not alter appreciably the true-breeding character of each race. Each race, therefore, is almost as uniform genetically as a clone, although successive generations are sexually produced. Furthermore, since each race is self-pollinating, a considerable degree of isolation is maintained between races. The first fact of importance, therefore, in an understanding of the taxonomic situation, is the existence of a great variety of true-breeding geographical races or biotypes, each more or less isolated by reason of its self-pollinating habit from other races.

(2) The second point is the fact that the isolation between races is not absolute. The barriers due to self-pollination can be overcome and are overcome from time to time. It has been found that sterility barriers do not exist between the various races of the North American euoenotheras. When artificially crossed, any race is able to form fertile progeny with any other race, the only exceptions being cases where plasma incompatibilities exist. In the field it has been noticed that insects often enter unopened buds in search of pollen and where they bring foreign pollen to a bud, or an open flower, whose anthers have failed for some reason to produce abundant pollen, it is probable that cross-fertilization takes place.

When such crosses occur, the hybrids which result appear to undergo a form of natural selection by which practically all hybrids which do not possess a ⊙ 14 are eventually weeded out. As I have pointed out elsewhere

(1940), ⊙ 14 probably has a sufficient survival value in comparison with other configurations to ensure its perpetuation at the expense of forms possessing some other configuration, since plants possessing this configuration will have a maximum of hybrid vigor coupled with abundant reproductive capacity resulting from the certainty of fertilization that goes with self-pollination. Furthermore, plants with ⊙ 14 require only a single pair of balanced lethals to enable them to breed true to this configuration, whereas plants with more than one circle would require balanced lethals in each circle if they were to breed true to their configurations. Since hybrids with ⊙ 14 are self-pollinating, and since they have balanced lethals and are able to breed true in respect to their configuration, there is no reason why they should not become the progenitors of new geographical races, each maintaining the same degree of isolation as is maintained by its parent race.

(3) The third factor in the taxonomic situation to be emphasized, therefore, results from the second. It is that new races may come into existence by hybridization, whenever the barrier between races is broken down by accidental cross-pollination, and a hybrid with ⊙ 14 and balanced lethals results. That this is a way in which new races are formed in *Euoenothera* is not mere surmise. The following facts seem to point to hybridization as a factor of prime importance in the origin of new races in this subgenus.

First, the complexes[4] which are associated to form a

[4] The term "complex," as used by the present author, has a somewhat broader meaning than the term "genome." It refers to a haploid set of chromosomes having a specific segmental arrangement as well as a definitive set of genes. If a complex becomes either segmentally altered or genically altered, it is no longer the same complex. Thus, *gaudens* (of *lamarckiana*) and *rubens* (of *biennis*) are identical segmentally, but not identical genically. They are, therefore, different complexes. On the other hand, the *albicans* of *biennis* and the *albicans* of *suaveolens* are identical segmentally, and essentially identical genically. The same complex is, therefore, considered to be present in these two races. If any cases were found where genic identity was accompanied by segmental diversity, it would be considered that two different complexes were also involved.

given race are not only dissimilar in segmental arrangement: they are frequently very diverse in genetic composition, as is shown by the diverse phenotypes which they produce when outcrossed to other forms. The fact that associated complexes are not closely related to each other cytologically or genetically strengthens the assumption that they represent diverse lines of evolution which have been brought together by outcrossing.

A second significant fact is the great similarity which exists between complexes of different races. Thus, while a given complex differs profoundly from the complex with which it is normally associated to form a plant, it may be identical in segmental arrangement and genetically similar to or identical with complexes in other races. We have turned up a number of cases where complexes with identical segmental arrangements exist in widely scattered races, being associated in one race with one complex, in another race with an entirely different complex. In most of these cases these cytologically identical complexes are also very similar to each other genically, while at the same time they are, in some cases, very different from the complexes with which they are associated. It is difficult to understand how a given complex can exist in more than one race, being associated with different complexes in the different races of which it is a part, unless this situation has been brought about by hybridization. A given race, with this particular complex, has crossed at various times with various other races, thus establishing a variety of new races carrying one complex in common. In all probability most euoenotheras with ⊙ 14 trace back to a hybrid origin, some complexes surviving in two or more true-breeding races thus formed.

It should be admitted, however, that some races may trace back only indirectly to a hybrid origin, for there exists the possibility that the complexes in a given race may become altered in one way or another in the course of time. For instance, interchanges may occur between associated complexes. Since the two complexes in a plant

are usually so diverse, an interchange between them may more or less profoundly change their genic and possibly their segmental characteristics. Such an interchange may be in the nature of crossing over in the pairing ends, which will not alter the segmental arrangements of the chromosomes making up the complexes; or it may involve reciprocal translocation between chromosomes of opposing complexes, which will alter the segmental arrangements of the complexes and thus create complexes which are new cytologically as well as genetically. It is also possible for an interchange between two chromosomes of the same complex to bring about an exchange of genes between the two associated complexes and the creation of cytologically and genetically new complexes (Cleland, 1942). In addition to these methods of alteration, there is also the possibility of the occurrence of point mutations. Because of the presence of balanced lethals, any recessive mutations which occur may be carried on from generation to generation indefinitely and will tend to accumulate to a point where the complex has become distinctly altered genetically.

There are ways, therefore, by which complexes can be altered. They can become altered in respect to genic composition while still retaining their own segmental arrangements. They can become altered both genically and in segmental arrangement. Thus it comes about that, while complexes in different races which are closely related from the standpoint of segmental arrangement are usually similar genetically, some exceptions are found. All this tends to complicate the situation somewhat—to increase the number of segmental arrangements existing in nature, and to break down to some extent clear lines of distinction between complexes of different ancestries and origins. It also results in occasional segregation of new types from old races, through the creation of gametes with new genetical and/or cytological characteristics. Some plants receiving the altered complexes may have less than ⊙ 14 and are not likely to survive, but others

may still have ⊙ 14 and thus be capable of giving rise to new true-breeding races which may carry new combinations of genetic and phenotypic characteristics. When one contemplates the possibilities of interchange that exist between associated complexes, and of genic alteration through the accumulation of point mutations, the wonder is that the situation in nature is not more complicated than it is. The fact that it is not more complicated indicates, in all probability, that these genetical and cytological alterations occur at the most with only moderate frequency.

(4) A fourth factor which influences the taxonomic situation is the fact that a majority of the dominant genes in a plant may be carried by one of the complexes, in consequence of which the phenotypic effect of the other complex is completely or almost completely hidden. There are many cases where this is so. Many of the broad-leaved "*biennis*"-type races carry a complex producing narrow-leaved *strigosa*-like plants when outcrossed to the proper race, as well as a complex producing broad-leaved plants. Other broad-leaved races do not carry such a complex, both of their complexes producing broad-leaved plants. It is very difficult, if not impossible, however, by mere external examination of a broad-leaved race to tell to which of these two categories it belongs—whether it carries a *strigosa*-like complex or not.

We can now see why it is that the task of determining relationships in the euoenotheras east of the Rockies becomes a difficult one from the purely taxonomic standpoint. This group is not made up of species in any sense in which this word is ordinarily used, and such entities as do exist do not lend themselves to classification by taxonomic methods. If we may summarize the facts just discussed, we will have a clearer picture of the sorts of entities which do exist:

(1) The population consists of a multitude of true-breeding races, often occupying the same area, but more or less isolated from each other because of their self-pollinating habit.

(2) Each race is a complex-heterozygote, containing two complexes which differ from each other in segmental arrangement and which are often very diverse genetically.

(3) These races are of hybrid origin, stemming from the infrequent occasions when the reproductive barriers have been transgressed; or they have been derived from such hybrid races as a result of modifications in genetic constitution or in segmental arrangement, which have followed gene mutation, crossing over or reciprocal translocation.

(4) One complex in a race is often masked by the other, so that its presence cannot be detected except by appropriate out-crosses. Hence, the relationships which a plant has through the masked complex will not be recognized unless such crosses are made. Nor can races which carry such hidden complexes be distinguished by external examination from those which do not.

It is evident that the groups which have the best claim to be considered valid taxonomic entities are the multitudinous geographical races which make up the general population. Should these be considered species? They have a degree of distinctness in that they do not ordinarily cross with other races. This is not, however, as clear-cut a barrier as exists in many other genera, for any race of North American *Euoenothera* is capable of crossing with any other, and of producing fertile progeny. The isolation which is maintained is due to the mere mechanical factor of self-pollination, and is in no sense as perfect as, let us say, in the case of the various species of *Drosophila*. When one couples this with the fact that these races are often too similar in appearance to be readily distinguishable and that they are so numerous, one begins to question the justification of calling such races "species." They are biotypes to which one might apply the term "microspecies," but they are certainly not the sorts of groupings with which the taxonomist can readily work. We are forced to conclude that, if there are no other groupings which can be called species in the population, the term "species" should not be used in connection with this assemblage at all. Are there, then, any other groupings which might conceivably be called species?

There is indeed some evidence of larger groupings, but, while some of these might possibly be handled with some

degree of satisfaction by the taxonomist, others could not be so handled. I will briefly review our present knowledge of these larger groupings.

We shall confine our attention to the euoenotheras ranging from Colorado eastward. Those to the west and south of this region have more or less normal cytological and genetical behavior and do not constitute a taxonomic problem too different from that found in other genera.

In general, we find that the western plains area is dominated by an assemblage of forms which have thick, narrow to moderately narrow, greyish green, and relatively uncrinkled foliage. This may be called tentatively the *strigosa* assemblage. This is replaced to the east by a plexus of plants with broad, crinkled, thin, clear green foliage, to which a variety of names has been applied, such as *biennis, pycnocarpa, nutans* and *laevigata.* In the southeast, along the Gulf Coast and spreading northeastward are plants with narrow, but dark, thin, clear green leaves which we may call the *grandiflora* assemblage, although most of them have flowers of moderate size. In the north-east, one finds a variety of forms which have very narrow, greyish or dark green leaves, with appressed or obsolete pubescence. The stems of these plants bend downward, then upward, at the tips in a characteristic fashion, and the buds have subterminal sepal tips. These may be referred to tentatively as the *parvifloras.*

While too few races have been studied for us to say definitely to what extent these groups grade into one another, or to what extent they are distinct, our impression is that the *strigosas* are fairly distinct from the *biennis* types, phenotypically, and the *parvifloras* are likewise reasonably distinct. The *grandifloras,* however, seem to grade rather insensibly into the broad-leaved types. It will be interesting to ask how these different groups behave cytogenetically, whether the individual races within a given larger group have common cytogenetic features, whether the races in different larger

groups differ cytogenetically, and whether any evidence of the existence of relationships between larger groups is obtained from cytogenetic studies.

Some seventeen races belonging to the *strigosa* assemblage have been studied in considerable detail, and it is found that there is considerable homogeneity in cytogenetic behavior in the group as a whole. Without going into detail, the following points characterize all the races so far analyzed. Each race has ⊙ 14 and balanced lethals. The complexes in a given plant produce similar phenotypes and may be rather similar genetically. One complex is transmitted through the egg (the α complex), the other through the sperm (the β complex). When these races are crossed out to the hookeris from California, either as male or female parent, hybrids with intermediate-sized circles are produced, indicating that both α and β complexes are removed by only three or four interchanges from the commonest *hookeri* end arrangements. Since the α complexes from different *strigosa* races can not be combined with each other as a rule, being transmitted only through the egg, nor can the β complexes, which are transmitted as a rule only through the sperm, it is not usually possible to obtain hybrids between two alpha or two beta complexes, but it has been possible to work out the segmental arrangements of quite a number of complexes in terms of certain defined standards, and it is found that the α complexes are very similar to each other in segmental arrangement, and the β complexes are also very similar to each other. In fact we have one case where two α complexes in different races are identical in segmental arrangement (both from Iowa), and we have two cases where two β complexes are identical (one case of identity being between a complex from Colorado and one from North Dakota, the other being between one from Colorado and one from Nebraska). An analysis of the segmental arrangements of the various complexes shows an entirely different history of interchange behind the α complexes on the one hand and the β

complexes on the other. The α complexes are all very similar to one another in respect to the interchanges which have produced them; the β complexes also show close similarities, but there are no cases known where interchanges have occurred between the same chromosomes in the formation of α and β complexes. It is evident that the α complexes have had a similar and perhaps a common origin and the β complexes have also had a common origin, but one different from that of the α complexes. It is probable that the strigosas represent the results of crossing between two overlapping and independently developed populations, one of which may have migrated into the region from the west coast, the other having spread northward from Mexico. Where the populations overlapped, crosses occasionally occurred and true-breeding hybrids were established which were the progenitors of present-day strigosas.

If this surmise is correct, it is probable that, in one sense, the strigosas have had only indirectly a common origin. Many crosses probably took place in different localities and the present-day strigosas probably stem from many independent crosses rather than from one. While they are alike in having arisen from the same two ancestral populations, they trace their ancestry back to a variety of independent beginnings. It is quite probable that the original populations were not entirely homogeneous cytogenetically and that the various strigosas were in some cases somewhat unlike in segmental arrangement and in genetic composition when they were first formed. The similarity between the various α complexes, however, which are presumably derived from one of the parental populations, and the similarity between the various β complexes, which are derived from the other parental population, do not allow us to assume any very great amount of heterogeneity in the races which crossed to produce the strigosas.

Turning now to the broad-leaved races, we find again more or less clear-cut types of cytogenetic behavior, but

these are, unfortunately for the taxonomist, not clearly correlated with differences in external appearance. From the standpoint of cytogenetic behavior these races fall into three groups, but it is not possible at present to tell with any degree of certainty to which group a given plant belongs by looking at it, since the plants are all broad-leaved and more or less similar in appearance. Up to the present time, 21 races have been studied belonging to group 1, 12 races belonging to group 2, and 4 races belonging to group 3. Much of the work on these forms has been done by Dr. Bayard L. Hammond and by Mrs. Louise Brandau Preer. In group 1, the α complexes carry genes for broad leaves and other so-called "*biennis*" characters, the β complexes carry genes for an essentially *strigosa*-like set of characters. In group 2, the α complex carries genes for *strigosa*-like characters and the β complex carries genes for "*biennis*" characters just the reverse of the situation in group 1. In group 3, both complexes are of the "*biennis*" type, producing broad leaves in outcrosses. In group 1, the α complexes closely approach the complexes of the *hookeri* alliance from the standpoint of segmental arrangement. In one race, the α complex has an arrangement identical with that of the commonest (ancestral ?) *hookeri* arrangement (that of [h]*Johansen*, etc.); in eleven races, its arrangement differs from this putative ancestral arrangement by but one interchange; in five races, its arrangement differs by a minimum of three interchanges. The β complexes of group 1, on the other hand, differ decidedly from the hookeris in segmental arrangement. None of those studied could have been derived from the [h]*Johansen* arrangement by less than three interchanges (one race), and most of them are more distantly related to this complex, differing from it by a minimum of four interchanges (two races), five interchanges (nine races) or six interchanges (three races). In group 1, then, the α complexes carry genes for "*biennis*" characters and are close to the hookeris segmentally; the β complexes carry genes for

strigosa-like characters and are far-removed from the hookeris segmentally.

In group 2, a complex carrying genes for *strigosa*-like characters is again associated with one carrying genes for "*biennis*" characters, but in this case, the former is the α complex and the latter is the β complex. With respect to segmental arrangement, the situation is not quite so clear-cut as in the case of group 1. The α complexes differ from the *Johansen* arrangement by a minimum of one (one race), two (one race), three (six races), or four (two races) interchanges; the β complexes differ by a minimum of three (four races), or five (six races) interchanges. In all cases where one complex is farther removed from the hookeris than its associated complex, it is the β complex which is farther removed. In group 1, it is also the β complex which is farther removed, but in group 1 the β complexes are the narrow-leaved ones, whereas in group 2 they are the broad-leaved ones.

In group 3, both α and β complexes carry genes for broad leaves and other "*biennis*" characters, and both complexes are moderately close to the hookeris in segmental arrangement, differing in all cases so far studied by a minimum of only two or three interchanges. It is as though the plants of this group were made up of two complexes similar to the α type in group 1 or to certain of the β type in group 2.

The three groups just characterized can not be distinguished from each other phenotypically with certainty. We are inclined to feel that we could, in a fair number of cases, pick out the wild races which carry two broad-leaved complexes (group 3), if they were brought into our garden, but we would find considerable difficulty in distinguishing between the other two groups. There is, however, a certain correlation between this grouping and geographical distribution. The group 1 races which we have studied were found for the most part in the Middle West, some of them, however, being found in the East. The following states are represented by this assemblage:

Arkansas, Missouri, Iowa, Illinois, Indiana, Kentucky, Maryland, Virginia. Group 2 races have come largely from the Northeast, the following states and provinces being represented: New Brunswick, Quebec, Ontario, Wisconsin, Michigan, New York, West Virginia, North Carolina. Group 3 has been found only in Virginia and North Carolina. It may be that the group 1 population has spread eastward from the Middle West, that the group 2 population has spread southward from the Northeast, and that these populations have overlapped in the region of Virginia and the Carolinas, resulting in the production of group 3 plants in this area, each carrying an α complex from group 1 associated with a β complex from group 2.

I referred earlier to the fact that complexes with the same segmental arrangement may exist in different races and that this is one indication of the hybrid origin of these races. We saw that there are some cases of this in *strigosa*. We have more striking cases among the broad-leaved forms. In group 1, there is one segmental arrangement which is so characteristic of the α complexes that it may prove to be more or less typical. This segmental arrangement exists in the α complex of nine of the twenty-one races so far studied. These nine races are found in Maryland, Kentucky, Indiana, Missouri and Arkansas—in other words, this segmental arrangement is widespread geographically.

Five of these nine races have β complexes which differ from one another in segmental arrangement. The other four races, residing in Maryland and Kentucky, have β complexes which are identical in segmental arrangement. Four races, therefore, are identical in the segmental arrangement of both complexes. It is interesting to note, however, that these races are quite easily distinguishable phenotypically. It is probable that genic changes not affecting segmental arrangement have occurred in their complexes since the time when the last alteration in segmental arrangement occurred, causing them to diverge

from one another genetically, while still retaining identical segmental arrangements.

In addition to these cases, several other cases of identity or near identity are known among the broad-leaved forms. It seems clear that the actual number of segmental arrangements is somewhat fewer than the number of races, some arrangements being found in more than one race. This serves to emphasize the probability that the various races have come into being through a process of hybridization.

With respect to the cytogenetic behavior of the *grandiflora* assemblage and the parvifloras little can be said as yet. The grandifloras grade to such an extent into the broad-leaved assemblage that no clear-cut line of demarcation has as yet been recognized. Cytogenetically all races so far examined have ⊙ 14 and balanced lethals. The complexes in any given race produce similar phenotypes—often distressingly similar, but one of them is close, or very close, to the hookeris segmentally, the other far removed not only from the hookeris but from every other complex so far analyzed. While only a few grandifloras have been examined, this general picture seems to characterize those which have been studied. Much more work will have to be done on the group, however, before it can be characterized with certainty.

The parvifloras are being studied by one of my students, Miss Lucie-Blair Hodges, but the work has not progressed far enough for definitive results to be announced. In general, the parvifloras, while differing greatly among themselves, seem to be fairly clearly demarcated from other groups. They all have ⊙ 14 and balanced lethals. In general they appear to have β complexes which produce bent stem tips and subterminal sepal tips, and which, when outcrossed, prevent the plastids of most other groups from developing chlorophyll. The latter characteristic makes it difficult to obtain hybrids between the β complexes of the parvifloras and complexes from other groups. Hence it will be difficult

to determine their segmental arrangements. The α complexes do not show a very close affinity segmentally to the *hookeri* alliance, but on the other hand they are not too far removed either. It is too early as yet to say more about their cytogenetic behavior.

From this brief survey, it is evident that the question which we raised, as to whether groupings exist which are larger than the numerous true-breeding biotypes, must be answered, with some reservation, in the affirmative. There is evidence of the existence of larger groupings with more or less distinctive cytogenetic behavior. If these groupings could be readily distinguished, the one from the other, on the basis of external appearance, there would be little objection to calling them species. The difficulty is that these groups can not in all cases be distinguished from one another. The grandifloras seem to merge insensibly into the broad-leaved assemblage, and the latter is made up of cytogenetically distinctive groups which are very difficult to distinguish phenotypically. It must be admitted that most of these larger groupings can not be handled with any degree of satisfaction by the taxonomist. We are forced to conclude, therefore, that the euoenotheras which reside from the Rocky Mountains eastward (and this constitutes the bulk of the North American euoenotheras) do not lend themselves, on the whole, to satisfactory taxonomic treatment. The larger groupings have for the most part vague and uncertain boundaries, and the multitudinous true-breeding and more or less isolated biotypes, most of which are with difficulty distinguished from their neighbors even in the experimental garden, are not the material upon which a satisfactory system of classification can be built. The best that taxonomists can hope to do is to create for convenience's sake a few categories which approximate as nearly as possible to the larger groupin which cytogenetic studies show to exist, admitting t' these will in some cases only vaguely correspond to t phylogenetically significant groupings which actually exist in nature.

It would seem wiser for taxonomists to adopt this conservative policy than to follow the procedure which has in some cases been adopted, namely that of giving specific rank to every biotype which enters the experimental garden, if it happens to look a little different from other biotypes previously observed by the grower. There are too many such biotypes to give each one a specific name, and giving names to the few which are brought under observation will tend to blind one's eyes to the existence of multitudinous forms which have not yet been studied, but which have as much claim to specific rank as those already named. It would be better to admit the unique difficulties in the situation and to adopt the simplest possible system of classification, admitting that clear-cut species in the usual sense of the word hardly can be said to exist in this group and that whatever system is adopted is bound to be but an approximation to the truth.

But while this situation can not be characterized as other than highly unsatisfactory from the standpoint of the systematist, it is of undoubted interest to the student of evolution. Here we have a group, apparently of recent origin, which has developed to a high degree a unique combination of characters—chromosome catenation, balanced lethals and self-pollination—constituting a mechanism which has profoundly affected the evolutionary development of the group. On the one hand a unique opportunity has been afforded for the accumulation of recessive mutations, including lethals, and these have probably accumulated in considerable numbers by this time. On the other hand, reproductive barriers have prevented to a large extent the mingling of genes which otherwise would have become distributed more or less widely throughout the population and would have given rise to diverse genic combinations with more or less survival value. Even when crosses have occurred, the resultant genic mingling has been limited, since for the most part only hybrids with ⊙ 14 have survived, and genic segregation has not taken place to a large extent within

such true-breeding types. It is perhaps not too far from the truth to say that the existent mechanism is such that it discourages the production of inter-racial hybrids, but when these are produced, those with ⊙ 14 tend to be perpetuated indefinitely, free from Mendelian segregation. Thus there has come to be a great diversity of types, but a different kind of diversity from that ordinarily found in freely interbreeding populations. Evolutionary progress in *Euoenothera* has followed and must continue to follow a somewhat different path from that pursued by other actively evolving groups.

In conclusion, it will perhaps be of interest to say a word about the cytogenetic situation in the South American euoenotheras and in other subgenera. So far as I am aware no cytogenetic work has been done hitherto on the South American euoenotheras. Through the kindness of Dr. Munz we have received seed of fifteen races of *O. campylocalyx,* one race of *O. elongata* and three races of *O. rubida.* One of my students, Mr. Charles W. Hagen, Jr., has been working on these and finds that this group shows many of the peculiarities found in the North American euoenotheras. The situation in these races may be very briefly summarized as follows:

(1) All races have shown fourteen chromosomes. Several chromosome configurations ranging from ⊙ 14 to seven pairs have been found; the situation seeming to be comparable to the situation in North America in that the majority of races have large circles, and most of the rest have seven pairs. Only one race out of nineteen has shown an intermediate configuration (⊙ 6, 4 pairs).

(2) Gamete lethals have been found in two strains, and balanced zygote lethals are present in all races with large circles. Races with large circles are in general self-pollinating, and those with seven pairs are open-pollinated, as in the North American euoenotheras.

(3) The strains classified as *campylocalyx* are extremely varied phenotypically. On the one hand, some bear a resemblance to *O. rubida;* on the other hand, some are close to *O. elongata.* It is probable that extensive investigation will show the same lack of clear-cut species that characterizes the bulk of the North American euoenotheras.

(4) The South American euoenotheras cross with great difficulty with the North American members of this subgenus. Successful crosses have been made with *O. affinis* (*Raimannia*) and it is possible that the South American euoenotheras are in reality more closely related to

the South American Raimannias than to the North American euoenotheras.

Mr. Hagen has also made a cursory cytological examination of certain other subgenera. He finds large circles in *Hartmannia* and *Lavauxia*. Small circles or wholly paired chromosomes are also found in races belonging to both groups. Little is known as yet of the genetic behavior or taxonomic peculiarities of these subgenera.

Another student, Dr. Adolph Hecht, has made a preliminary study of the subgenus *Raimannia*, having examined a total of 53 races involving 14 of the 19 listed species, the seed for which was kindly furnished by Dr. Munz. In *Raimannia*, the species seem to be more clearly delimited than in *Euoenothera*. There is, however, considerable variability within species, numerous geographical races being present. The cytological peculiarities found in *Euoenothera* are also present in *Raimannia*, but not in so striking a degree. About 64 per cent. of the races examined have had ⊙ 14, and about 26 per cent. have had seven pairs, the remaining 10 per cent. showing intermediate configurations. Within a given species quite a variety of configurations may be present, ranging from ⊙ 14 to seven pairs. Balanced lethals are apparently present in the forms with large circles. While the analysis has not proceeded far enough to make possible definite conclusions, it is probable that there has been less of a tendency toward the production of biotypes isolated by reproductive barriers, such as are found in *Euoenothera*, since self-pollination is not so widespread a phenomenon. The evolution of the Raimannias partakes less of the peculiarities of the euoenotheras and appears to follow a more conventional pattern. The details of this situation have not been worked out as yet, however.

From this extremely preliminary excursion into the cytogenetics of other groups of the genus *Oenothera* it is apparent that the cytogenetic peculiarities found in *Euoenothera* are not confined to this subgenus alone, but are more or less widely distributed among the other sub-

genera. They are also found in certain other genera of the family Onagraceae. Whether any other group carries these peculiarities to such an extreme as do the North American euoenotheras, however, remains to be seen.

Summary

Except for those forms growing in the southwestern portion of the United States and contiguous areas, the North American euoenotheras do not show a clear-cut segregation into readily recognizable species. Instead, the population consists of a multitude of geographical races which because of balanced lethals breed true, and because of a self-pollinating habit maintain a considerable degree of isolation from each other.

Each race is a complex-heterozygote, whose two complexes differ from each other both in segmental arrangement and in genic composition.

These races are of hybrid origin, owing their origin to the infrequent occasions upon which the reproductive barriers have been transgressed; or they have been derived from such hybrids through subsequent alteration in segmental arrangement or in genetic composition.

One complex in a race often masks the phenotypic effect of the other complex, so that the presence of the latter, and the relationships which this race bears through the latter, can only be shown by outcrosses.

These races fall on the basis of cytogenetic behavior into larger groups. These are the comparatively narrow-leaved forms of the western plains area, the middle-western broad-leaved forms, the north-eastern broad-leaved forms with difficulty distinguishable phenotypically from the middle-western ones, a third broad-leaved group found in Virginia and North Carolina, the grandifloras of the southeast coastal plains area and the parvifloras of the north-east. These groups can not always be distinguished from each other with any degree of certainty on the basis of phenotypic characters and, hence, are of little value to the systematist. They show

distinctive cytogenetical behavior, however, and constitute the nearest approach to species in the usual sense of the word to be found in the assemblage.

The major factors which have brought about this situation have been (in addition to gene mutation) segmental interchange leading to circle formation, the development of balanced lethals, the acquisition of a self-pollinating habit resulting in the erection of reproductive barriers between races, and the occasional transgression of these barriers through outcrossing leading to the origin of new races. Evolutionary progress in this group has, therefore, followed a rather different pattern from that found in other organisms.

The cytogenetic situation in the South American oenotheras, so far as this is known, is briefly summarized and compared with the situation in the North American euoenotheras.

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THE EARLY HISTORY OF THE AMERICAN NATURALIST[1]

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THE first issue of *The American Naturalist, A Monthly Magazine of Natural History,* appeared in March, 1867. It is thus sixteen years older than the American Society of Naturalists, which was organized in 1883. The relations of the society to the magazine have always been close. Its editors and associate editors have been almost invariably members of the society and two of the founders of the magazine were also founders of the society. At the third meeting of the society in Boston in 1885 THE AMERICAN NATURALIST was made the official organ of the society for publication, and so far as I can discover that act has never been rescinded. It is therefore appropriate that some important events in the history of the magazine should be brought to the attention of the members of the Society of Naturalists.

THE AMERICAN NATURALIST was started, soon after the close of the war between the States, by four men who had been students of Louis Agassiz and assistants in the Museum of Comparative Zoology at Harvard College. These men were Alpheus S. Packard, Jr., Frederick W. Putnam, Edward S. Morse and Alpheus Hyatt. All of them had been assistants in the museum for several years, and two had left to serve in the Union Army, Packard as assistant surgeon in the 1st Maine Volunteers and Hyatt as captain in the 47th Massachusetts Regiment. They were therefore men of maturity as well as enthusiastic naturalists. Their positions at the Museum of Comparative Zoology were much like those of graduate assistants in our present universities. They attended lectures by

[1] This paper was prepared for the annual meeting of the American Society of Naturalists, which was scheduled to be held in New York City on December 29, 1942, but was cancelled owing to war conditions.

Professor Agassiz and worked on the collections in the museum, each in his own chosen field. Their relations with the professor were in general cordial, in some cases almost worshipful, but they were mature men, desirous of making careers for themselves and of becoming self-supporting. Their pay was small, and their hours long. It is known that Packard received $400 a year and the others probably similar amounts. Each of them had problems of his own which he wished to work on, but museum duties left little opportunity for independent work. Under these circumstances it is not surprising that discontent arose. Agassiz was unable to increase their pay, his own salary at the time is said to have been only $1500 a year, and he felt that his assistants should devote their working time to the museum.

The spirit of independence in the assistants reached a climax when a sheet of "Regulations for the Museum of Comparative Zoology" was posted, which was designed to prevent assistants from working on their own problems during museum hours. As a result five of the older assistants swarmed out of the museum hive; Addison E. Verrill went to the Smithsonian Institution, and later to Yale, while Packard, Putnam, Morse and Hyatt went to the old Essex Institute and the new Peabody Academy of Science at Salem, Mass. Nathaniel Shaler was urged to join them, but he declined, saying that he had just finished putting down one secession (in the Civil War) and was not going to join up with another. Packard later became professor of zoology at Brown University; Putnam professor of anthropology successively at Chicago, California and Harvard; Hyatt became curator of the Boston Society of Natural History, while Morse continued to the end of his long life as director of the Essex Institute and Peabody Academy at Salem.

Putnam was a nephew of George Peabody, a native of Essex County, who had made a great fortune as merchant and banker before moving to London and whose benefac-

tions established Peabody Institutes in several American cities. Putnam was director of the Essex Institute from 1864 to 1870, and probably knew in advance of his uncle's intended gift to the Essex Institute, for in 1866 he had written to Morse, Hyatt and Packard that by the fall of that year they would be offered employment there. The founding of the Peabody Academy of Sciences and the starting of THE AMERICAN NATURALIST are well described by Dorothy G. Wayman in her excellent book, "Edward Sylvester Morse,"[2] from which I quote the following sentences:

> On February 26, 1867, George Peabody placed in the hands of the trustees of the Essex Institute $140,000 "for the promotion of science and useful knowledge in the county of Essex," and he provided that the Institute and the East India Marine Society be combined. Thus the Peabody Academy of Sciences came into being and in May, 1867, Morse, Hyatt and Packard became members of the staff, of which Putnam was already Director.
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> On November 22, 1866, these four men drew up an "Agreement of the Editors of THE AMERICAN NATURALIST," which begins:—"The following expenses are to be paid first and in the following succession: 1. Paper, 2. Printing, 3. Engraving, 4. Binding, 5. Incidentals, 6. Advertising, 7. Drawing, 8. Chief Editor's actual expenses for the year, board, clothing, traveling. Should any money remain after the above expenses are paid, this amount will be divided among the Editors according to the amount of their contributions pro rata." . . . Packard looked after the publishing details; Hyatt kept the books, and Morse, as secretary, had charge of the mailing list and subscriptions. Their first printing was of 250 copies. The Magazine was published [by the founders] until 1878. It never made its editors rich, but it was the first publication to combine science and popular interest and to use artistic illustrations for scientific articles. Packard wrote most of the articles, and Morse made most of the drawings . . . Putnam was indefatigable in his work for the NATURALIST, correcting proof, and finally establishing a printing office known as the Salem Press.

Although Packard was chief editor it is certainly not true that he wrote most of the articles. The first volume of 680 pages contained 47 principal articles by 39 authors (of which Packard wrote 5, Morse 2, Hyatt 1), 23 reviews of current works on natural history, 26 shorter articles or notes on botany, 38 on zoology, 11 each on geology and mineralogy, 9 pages of a natural history calendar for the

[2] Harvard University Press, 1942, pp. 211–216.

different months, 18 of correspondence and reports of the proceedings of scientific societies, and finally 8 pages giving a glossary of scientific terms used in the volume.

The introductory statement in the volume says that "The NATURALIST aims to be a scientific monthly addressed to all lovers of nature; it is hoped that it will be equally welcome to farmers, gardeners, and artisans. Its aim is practical and economic as well as theoretical." Thus the NATURALIST was intended to be not only a general scientific magazine but also a journal of scientific news, for at that time there was no other publication in America performing these services. Later as various technical journals were established they took over publication of much of the research work in the natural sciences, while *Science*, *Popular Science Monthly* (now *Scientific Monthly*) and other popular journals in various fields of science took on some of the many functions which the NATURALIST initially performed.

In this process of differentiation the history of the magazine is not unlike that of the Society of Naturalists. Just as the latter gave rise by gemmation to the Association of Anatomists and to the Geological, Physiological, Morphological (now Zoological), Psychological, Botanical and Bacteriological Societies, so THE AMERICAN NATURALIST has budded off the various journals of all these societies. The question is sometimes asked whether there is any present need for a Naturalist's Society or journal. However, in all life and development integration must accompany differentiation and there is now a growing interest in the general and philosophic aspects of science. Furthermore, there is need of a journal which specializes in the more general fields of natural history. When the question was asked, several years ago, whether there was any further work for the American Society of Naturalists, it was the general opinion that it served a very useful purpose by bringing together workers in botany, zoology, geology and the natural sci-

ences in general and providing a forum for the discussion of problems common to all of them. One of the most general of all problems of the natural sciences is evolution, and at the Baltimore meeting of the Society of Naturalists in 1908 it was voted "that the study of evolution be the general policy of the Society, unless otherwise ordered." This "temporary plan" has now become the settled policy of the society, evolution being properly interpreted to include genetics, cytology and biochemistry, as well as the more usual fields of speciation, adaptation, distribution and in general the philosophy of the natural sciences.

In like manner the field of the journal, AMERICAN NATURALIST, has of late followed the policy of the Society of Naturalists. The symposia at the meetings of the society are usually printed in the journal and are generally of a high order of excellence. Other contributions that are published in the NATURALIST are usually of such importance that it is widely recognized as one of the leading scientific journals of America. Although it is not owned by the Society of Naturalists it is still its "official organ for publication," as it has been since 1885.

The first three volumes were edited by A. S. Packard, Jr., E. S. Morse, A. Hyatt and F. W. Putnam; volumes four and five were edited by Packard and Putnam, while Morse and Hyatt were associate editors and thereafter their names disappear from the editorial staff. Volumes six to nine were edited by Packard and Putnam, with R. H. Ward, associate editor for microscopy. With volume ten and eleven Packard alone appears as editor, with R. H. Ward and G. H. Goodale as associate editors.

The first nine volumes were published in Salem, Mass., the first by the Essex Institute and the others by the Peabody Academy of Sciences. Volumes ten and eleven bear the imprint, "Boston: H. O. Houghton and Company." The last paragraph on the last page (758) of volume eleven carries the following, "IMPORTANT ANNOUNCEMENT

TO SUBSCRIBERS. THE AMERICAN NATURALIST will hereafter be published by Messrs. McCalla and Stavely, Philadelphia, Pa., and will be edited by A. S. Packard, Jr., and Prof. E. D. Cope, with the assistance of eminent men of science."

It is evident that all the original founders and editors, except Packard, had grown weary of the editorial work and that the publishers had not found the NATURALIST a profitable venture. Under these circumstances Cope acquired ownership and undertook the business management as well as editorial supervision. Cope was not a business man nor a meticulous editor; he was too busy with scientific expeditions, writings and other matters of greater moment to pay much attention to the Philadelphia publishers, and probably Packard was too far away. The editorial policy was so generous, and the possible outlets for publication so restricted, that the monthly magazine grew to giant size, many annual volumes running to 1,200 pages or more. The costs so far exceeded the intake that the journal began to be a heavy financial burden and Cope was in frequent difficulties with his publishers. McCalla and Stavely published Vols. 12–19, later volumes were published by several different firms. As a result the NATURALIST often appeared irregularly and tardily.

But its editorial support and scientific value were maintained at a high level. Packard continued as editor until Volume 19, 1885, when he withdrew. He had been the principal editor for eighteen years. With Volume 20, 1886, J. S. Kingsley took Packard's place as co-editor with Cope and continued in that position until after Cope's death in 1897. At various times during Cope's management all the following persons were associate editors, usually for brief periods: E. A. Andrews, W. S. Bailey, C. E. Bessey, R. P. Bigelow, Elliott Coues, J. H. Comstock, W. H. Hobbs, F. C. Kenyon, F. S. Lee, H. C. Lewis, W. N. Lockington, H. C. Mercer, T. H. Morgan, O. T. Mason, W. A. Newbold, C. V. Riley, J. A. Ryder,

W. T. Sedgwick, Henry Seward, Erwin F. Smith, R. H. Ward, H. C. Warren, Clarence Weed, C. O. Whitman, G. H. Williams, Thomas Wilson, J. L. Wortman, Ellis Yarnell—twenty-eight in all, representing almost every branch of biology and geology. The wide interest in the NATURALIST could not be better shown than in this list of associate editors.

During the nineteen years that Cope owned the journal, 1878–1897, the entire list of his own publications included more than 900 papers[3]; of these 776 were published in THE AMERICAN NATURALIST, and 122 of them were editorials on many themes of current interest which appeared in a section called "The Editor's Table." Many of these editorials have present-day interest and deserve to be more widely known; all of them are interesting, many scintillate with wit, sarcasm, humor, for Cope had the habit of speaking "out of his liver and jaw." His last editorial was found on his desk after his death in April, 1897, and was printed in the NATURALIST for July of that year.

After the death of Cope, J. S. Kingsley continued as editor for three months and then R. P. Bigelow succeeded him. The August number for 1897 contained the following notice (pp. 699, 700): "CHANGE OF OWNERSHIP: THE AMERICAN NATURALIST has been purchased from the estate of E. D. Cope by a number of gentlemen who are interested in the advancement of the natural sciences. Dr. Robert Payne Bigelow, of the Massachusetts Institute of Technology, has accepted the post of editor in chief. He will be assisted by an Editorial Committee and by an able board of Associate Editors, whose names will be announced later." These associate editors were J. A. Allen, E. A. Andrews, W. S. Bailey, C. E. Beecher, D. H. Campbell, J. H. Comstock, W. M. Davis, D. S. Jordan, C. A. Kofoid, Chas. Palache, D. P. Penhallow, M. H.

[3] See Henry Fairfield Osborn, "Cope, Master Naturalist." Princeton University Press, 1931.

Richards, W. E. Ritter, F. Russell, L. C. Russell, Erwin F. Smith, L. Stejneger, W. Trelease, S. Watase—truly a notable list of names.

The names of the gentlemen who purchased the journal from the Cope estate and of the editorial committee were not made public, but inquiry among some of the survivors indicates that one of the prime movers was the late Dr. W. McM. Woodworth, of the Museum of Comparative Zoology, and that C. B. Davenport and G. H. Parker were associated with him. R. P. Bigelow was editor beginning with the September number of 1897 and ending with the December issue of 1898. Thereafter no names of editors were published, but Dr. Bigelow remembers that Woodworth followed him as editor and that Parker took Woodworth's place when he was absent on expeditions with Alexander Agassiz. During this ten-year period from 1897 to 1907 the NATURALIST was kept alive and edited by this group of men at Harvard, the Massachusetts Institute and Tufts. It was published by Ginn and Company, Boston.

In 1907 J. McKeen Cattell acquired the NATURALIST and has continued to edit and publish it ever since, although his name did not appear as editor until 1925. Since 1939 Jaques Cattell has been associated with his father, and is now the responsible editor. In accordance with action taken at the annual meeting of the American Society of Naturalists held in Philadelphia on January 1, 1941, a committee drew up a plan for the organization of a board of consulting editors. The following have consented to serve in that capacity: W. C. Allee, University of Chicago; G. W. Beadle, Stanford University; L. J. Cole, University of Wisconsin; Th. Dobzhansky, Columbia University; C. L. Hubbs, University of Michigan; C. W. Metz, University of Pennsylvania; Karl Sax, Harvard University; A. Franklin Shull, University of Michigan, and L. J. Stadler, University of Missouri.

For more than fifty years the journal appeared as a monthly; in 1918 it was issued as a bi-monthly and has

so continued. A study of its seventy-five volumes shows that it contains a great store of valuable material, much of which is overlooked because of the lack of a comprehensive index of the entire series. May this lack be remedied soon! As this oldest and best of American journals of natural history goes into the last quarter of its century, the American Society of Naturalists hails it with Rip Van Winkle's blessing: "May you live long and prosper!"

THE NATURALIST IN AMERICA[1]

DR. L. C. DUNN

SEVENTY-FIVE years ago there appeared the first number of a natural history journal which has since become the oldest American scientific periodical in its field. It was called *The American Naturalist—a popular illustrated magazine* and the names of its editors and of its contributors and the nature of its contents all indicate clearly what a "naturalist" was in those days. He was one who studied animals and plants. He might also be interested in minerals or weather or stars, but this interest was nearly always connected closely with animate nature. His method was primarily observation and description, in nature, for it was a time of exploration, of listing the animals and plants of the world, of study in the field, and there were few laboratories of zoology or botany in which any other method could be followed.

Many of those who published their observations in the NATURALIST had no academic connection. They were professional or business or literary men or men of leisure. As naturalists they were amateurs and the love they bore the study of natural history shines in many of the papers in that first volume. Both the contents and style of many of the papers in the early volumes show that those who wrote them were not pressed for time or hounded by ambition; they had the leisure to put their observations and questions into the polished literary form of the day. They owed their leisure, in part, to the commercial prosperity of the nineteenth century. Naturalists, in those

[1] Introductory remarks of the chairman of a symposium which the American Society of Naturalists had planned to hold at its meeting in New York in December, 1942. The symposium, which was to have had as subject "The Naturalist in America 1942 ± 75, Retrospect and Prospect," was intended to mark the seventy-fifth anniversary of the founding of THE AMERICAN NATURALIST. The meetings of the society were cancelled at the request of the Office of Defense Transportation. Two manuscripts intended for presentation at the symposium have been received and appear herewith. Others may appear in subsequent issues.

days, often had incomes and could afford the leisure. In the same year when the NATURALIST began publication, young Alexander Agassiz met the young Professor Charles W. Eliot in the streets of Boston. He said:

> Eliot, I am going to Michigan for some years as superintendent of the Calumet and Hecla Mines. I want to make money; it is impossible to be a productive naturalist in this country without money. I am going to get some money if I can and then I will be a naturalist. If I succeed, I can then get my own papers and drawings printed and help my father at the Museum.[2]

Agassiz made a lot of money and became a good naturalist.

In some of the papers sentimentality passed for love of nature and in only a few the purpose to be served was "science." The arts of observing, of recording, of cataloguing, of preparing specimens, of taxidermy, of adapting the new method of photography to the naturalist's needs stood before the science. It is the glory of the truly great naturalists that they make us forget the distinction between the art and the science, and a few of the early NATURALIST papers achieve this synthesis.

A shining example of the amateur naturalist stood before all in those days, one who by reason of inherited wealth could afford to be a naturalist and who by diligence and breadth of observation turned the art of the naturalist into a new foundation for all the biological sciences and created a new freedom for thought and speculation. "The Origin of Species" preceded the first volume of THE AMERICAN NATURALIST by only eight years; and Darwin's evidence as contained in "The Variation of Animals and Plants" appeared and was reviewed promptly in Volume 2. Darwin's views had certainly not prevailed in 1867, for the address of the president of the American Association for the Advancement of Science, Professor J. S. Newberry, was printed in Volume 1 of the NATURALIST and it contained these lines:

[2] "Letters and Recollections of Alexander Agassiz," p. 61. Edited by G. R. Agassiz. London: Constable and Co. 1913.

This much I have said in view of the possible acceptance of the Darwinian theory by the scientific world. I should have said, *in limine*, however, that the Darwinian hypothesis is not accepted and can never be fully accepted by the student of science who is inspired with the spirit of the age. From the nature of things it can be proved only to a certain point, and while we accept that which is proven,—and for it sincerely thank Mr. Darwin,—that which is hypothesis, or based only upon probabilities we reject, as belonging in the category of mere theories, to disprove or purify which the modern scientific reform was inaugurated.[3]

There were great naturalists in this great tradition then working in America and the new journal had to represent the interests of men like Agassiz, Cope, Coues, Dana, Hyatt, Leidy, Marsh, Packard and others of equal stature.

The activity of naturalists was coming into fruition in many ways in those days. The zoological museum at Harvard was new (begun 1859), the American Museum of Natural History was founded in 1869, and the summer settlement at Penikese Island, which gave rise to the Marine Biological Laboratory at Woods Hole, was founded by Louis Agassiz in 1873.

That was three quarters of a century ago. To-day THE AMERICAN NATURALIST still appears. Its nine consulting editors are all professional biologists from the universities, and seven of them represent fields of work which did not exist when the NATURALIST began, namely, genetics and cytology. In the issue for November–December, 1942, the eight papers all deal with genetical or cytological problems. The significant fact, however, is that all of them are concerned with the factors of evolution and this has been and continues to be the inquiry which unites and inspires naturalists. If these are "laboratory" papers (and all of them are) it only means that in 1942 the naturalist may work with the methods of 1942; and these must perforce be different from those of 1867. THE AMERICAN NATURALIST has become a profes-

[3] J. S. Newberry, THE AMERICAN NATURALIST, 1: 464, 1867. Annual address of the president, delivered at the meeting of the American Association for the Advancement of Science held at Burlington, Vermont, August, 1867.

sional journal. By no stretch of meaning could its 1867 masthead, "a popular illustrated magazine," describe its character to-day. The amateur naturalist has virtually no place in its pages, and art, by and large, has been replaced by science.

The changes in THE AMERICAN NATURALIST illustrate what has been happening to biology generally in the United States. In these 75 years there have arisen many methods of study largely of a quantitative experimental nature which must be pursued principally in the laboratory. The goal of these studies appears to be analysis, rather than the synthesis which stood more immediately before the older naturalists.

These different methods of modern biology have led to apparent differences of purpose amongst the scientific descendants of those who called themselves naturalists. There are those whose interest clings to animals and plants as such, to the time-tested methods of observation in nature and to the older questions of evolution, phylogeny, selection, adaptation. There are others who, under the influence of physics and chemistry, hope to reduce the laws of living matter to the same terms of matter and energy which have proved themselves so universal in the other natural sciences. Some biologists of this persuasion tend to think that the day of the older naturalist is over; that the questions of the future will find their answers only as a result of radical experimental analysis. To this the upholders of the naturalist tradition retort (or seem to) that continued analysis, like hope deferred, sours upon itself, and, by gaining its satisfaction from minor facts, however exactly demonstrated, moves away from rather than towards the problems presented by animals and plants in nature. Since this apparent division among biologists has been recognized by so many, it has seemed to offer a good topic for discussion at this celebration.

This division may already be a thing of the past, for there are now many who study the old questions with the

new tools, and for these there has always been and I suppose always will be a place in THE AMERICAN NATURALIST. They probably represent the naturalists of to-morrow.

On such an anniversary all students of nature may well ask themselves whether their purposes, their ideals and their hopes have changed; whether the new methods have brought new understanding of nature; whether they are content to pursue them in the new ways which are now themselves becoming old ways. There is a farther question which the readers and contributors to THE AMERICAN NATURALIST of 1942 must face. How will the naturalist tradition fare in the hard new world that is being born out of the war? These are questions with which the speakers in this symposium must wrestle.

While we gather to recall the fruitful history of this journal, we can take comfort for its future by contemplating its past. Its past has been good, partly because it has endured as a continuous thread connecting us with good naturalists of another day. We may wish it well for the next 75 years, seeing in the continuity of its purpose, apart from all the inevitable changes of its form and method, our best assurance of future good.

THE FUTURE OF THE NATURALIST[1]

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IF we choose to go by the lexicon, a naturalist is any student of natural sciences, no matter what technique he employs or how restricted the field of his specialty. In that sense of the word I am sure you will agree that the naturalist has quite a future, as well as a most respectable past.

If this were an ordinary tribunal, that should end the debate. We are, however, a group of natural scientists not content to accept written authority unless we can verify it from our own observations. And we have observed that many of our colleagues in the natural sciences do not consider themselves to be naturalists at all. This is certainly true of astronomers, physicists and chemists. It is increasingly true of geologists and biologists. So, regardless of the dictionary, something is happening to the word "naturalist." It becomes our business to find out what sort of change is going on, and to clarify the situation if we can.

So long as a language is alive, its words are malleable. The only exceptions are those words, *e.g.*, scientific terms, whose meaning is fixed by formal agreement. Yet every one of us who has worked behind the façade knows of instances where the tempering of a scientific term has involved more of rough-and-tumble than of either formality or agreement. I suspect this to be true of the term under consideration. It has an explicit definition of long standing, but we are not satisfied to use it in that sense. Its meaning has obviously been restricted. I am certain that in some quarters it has been degraded. Against this latter change I protest, and on that issue fix the debate.

[1] This paper was prepared for the annual meeting of the American Society of Naturalists, which was scheduled to be held in New York City on December 29, 1942, but was cancelled owing to war conditions.

The classical division[1] of knowledge upon which our faculties have been constructed is four-fold. All recorded fact is history, its meaning is philosophy. All knowledge of man is moral, all else natural. By combination we have:

Moral history—the record of man.
Moral philosophy—the significance of this record.
Natural history—the record of nature, excepting man.
Natural philosophy—the interpretation of nature, excepting man.

In practice, while natural history concerned itself with observing the heavens, the earth and living organisms, natural philosophy was concerned with speculation about them. This speculation led to the mathematical analysis of astronomical observations, whereupon the astronomer ceased to regard himself as a natural historian. It led to chemical and physical experiment, whereupon the doctors concerned began to consider themselves natural philosophers. Natural history was left with only the botanists, zoologists and geologists on its hands, and to these practitioners the word "naturalist" was restricted.

As botany, zoology and geology have become increasingly technical and experimental in character, they too have dropped the rubric of natural history. Many of the scientists concerned seemed content, unless I am mistaken, to regard the term as obsolete or to use it as an *omnium gatherum* for any sort of superficial, uncoordinated study of nature that is out-of-doors and does not involve the use of apparatus. Also, if my observation is correct, the term "naturalist" has undergone, in the minds of many, a parallel change.

The distinction between a record and its meaning is still as valid as it ever was. History is one thing and philosophy another. But the course of science shows that the two can not, in practice, be divorced. The scientist, in seeking new facts, must be guided by the meanings already in his possession. He must, whatever his discipline, be at once natual historian and natural philosopher.

[1] *Cf.* Sir David Prain, *Ann. Applied Biol.*, 8 (1): 66–76, 1921.

More than that, man can not always be considered apart from the rest of nature—probably not ever. The natural scientist can not avoid the fringes of moral history. As to moral philosophy, that is something no scientist can escape. The very decision to avoid it is a moral judgment.[2]

The elaborate specialization of knowledge may seem to have broken the four classical fields into fragments. This is an illusion. The efforts of specialists, consciously or otherwise, have instead blended them into a unity and broken down the once distinct walls between them. In this flux, what remains *of* the naturalist and what remains *for* him? To get at this problem I propose to consider an authentic, confessed and conceded, naturalist, Charles Darwin. Does he represent something once useful and vital, but now on its way out, like the ivory-billed woodpecker? After all, that is a fair question, for he himself remarked, "We need not marvel at extinction."[3]

The greater part of Darwin's working life was unquestionably devoted to natural history. He called himself a naturalist, and so he was. He observed living plants and animals and their environment. He observed, too, the records of the past. This did not prevent him from reflecting upon what he had seen—from behaving like a natural philosopher. Nor did it prevent him, when he saw good reason, from undertaking experiments. Some of these periods of experimental work were prolonged and the experiments were elaborate.[4] I am not aware

[2] An old saying, variously attributed, runs "Every man is a philosopher. For if you say, 'I am not a philosopher,' that is a philosophic judgment." In commenting on this A. Meiklejohn (personal communication) writes: "If I were making the assertion now I'd say, 'The man who denies he is a philosopher is one if he knows what he is saying, because, to know it, he must know what philosophy is; and if one knows that, one is a philosopher.' You see I leave out the people who neither affirm or deny it. Some people seem to come fairly close to absence of activity on the subject."

[3] C. Darwin, "The Origin of Species." Sixth edition. New York, 1883. P. 297.

[4] *Cf.* C. Darwin, "The Power of Movement in Plants." New York, 1881.

that he considered himself the less a naturalist for that reason, although again he was behaving as a natural philosopher rather than a historian. A physiologist does not cease to be what he is when he steps out-of-doors to see if his experimental results on nutrition or sensory responses can be applied to situations occurring under field conditions. He remains a physiologist. The laboratory door does not lock behind him and bar his return any more than it swung shut to imprison Darwin and forever cancel his status as a naturalist.

The distinctive thing about the work of Darwin, the naturalist, is not to be found wholly in his technique of observation and record. More deeply, it lay in his direction of approach to the unknown. He came at it, not from a single point of structure of behavior, but from the integrated picture of living nature. Of necessity he dealt with massive groups of complicated factors. Some of them he resolved. Others have been brilliantly analyzed by more modern workers. Some remain a challenge to our skill and cerebration. It would be a harsh judgment that called him superficial because he neither began at the small end nor awaited all the answers in detail.

There are parallel situations in other fields of science. No one would call builders of organic chemistry superficial because they were obliged to proceed with their work in the absence of a proper electron chemistry. Indeed they had to go ahead without being able to rationalize organic with the simpler inorganic chemistry. In mathematics the very power and beauty of the higher methods lie in their ability to "get behind what is behind" and deal with massives in advance of detailed analysis and computation. This is not to question that modern genetics, for example, has been necessary to illuminate, even to modify, the ideas of Darwin on variation. In a sense the detailed and critical work of the laboratory must always be a court of last resort. But that it is a sufficient source of scientific truth or the source of a higher kind of truth may at least be questioned. The

great relationships remain in living nature, facts as uncompromising in themselves as the swing of a galvanometer or the splitting of a chromosome.

It was clear from Darwin's work that there had to be a science of heredity and variation. This indeed he predicted[5] and labored in his later years to develop, handicapped by his apparent ignorance of an obscure pamphlet from Bohemia. Later it seemed perfectly fitting for a group which called itself the American Society of Naturalists to devote its powerful sponsorship and many of its finest programs to the infant science of genetics. And the naturalists hung on, and kept their name and their sponsorship long after this science became one of the most intricate, precise and abstruse fields of experimental work. They saw it through, whether they all saw through it or not. I, for one, lost the thread some years ago, to my profound regret.

Certainly the idea of continuous descent and variation was near the heart of Darwin's work. But beneath it lay another idea even more fundamental—the inseparability of life and environment. Actually this idea was implicit in the first studies on material interchange and metabolism which began with the study of oxygen more than seventy years before "The Origin of Species" appeared. Darwin gave to it a proper emphasis and universality in the study of living organisms. Thereafter it became inconceivable to contemplate life divorced from the environment except as a matter of temporary convenience within the laboratory. It became inevitable, and should have been obvious, that there had to be a scientific discipline which approached biology as a problem of interrelationship of organism and environment. Darwin's own studies were a shining example of such an approach. The parentage of this new science was as august as that of genetics—indeed it was the same. But while the latter

[5] C. Darwin, "The Origin of Species." Sixth edition. New York, 1883. P. 426. "A grand and almost untrodden field of inquiry will be opened, on the causes and laws of variation, etc."

infant was publicly acclaimed, the former was slipped into the temple of learning through a side door and mumblingly christened "oecology."

Intrinsically, and from the standpoint of euphony, there should be nothing wrong with this term. Yet I marvel at its capacity to draw blank looks from the average layman, to say nothing of an occasional black look from the ordained. I saw a dean, himself a scientist, amazed at the erudition of a new college president who used the word familiarly in conversation. The dean afterwards (for he was a bluntly honest fellow) confessed that he did not know there was such a subject as ecology. Enlightened publicists, including H. G. Wells, Patrick Geddes, Lewis Mumford and Henry Wallace, have tried to get the word into familiar usage. Yet, not long ago, a discussion among congressmen boiled down to the question, "What [the hell] is ecology?"

For a time only two universities, both of them young and brash, gave the subject house-room in the United States. As recently as 1917, the biologists interested in this approach to their subject got such scant consideration from their parent societies that they had to organize their own. A number of the great universities still ignore ecology or accord it the bar sinister and tolerate it. One distinguished man, now dead, who was head of a great department, is on record as having written that he wanted a new man and it made no difference what his special interest was except that he did not propose to have an ecologist around.

I have made some effort to discover the retarding factor. There are of course crowded curricula, vested interest (which is another name for economic fear), preoccupation with other interests and on occasion, personalities which operate adversely against any new subject. These I pass by. More serious are two opinions: one, that ecology has no intellectual content or *raison d'être,* and is but the superficial emphasis of what every man knows; two, that it is the capsheaf of biological work

and no one has any business meddling with it so long as we are so ignorant of many details which must be attended to first. While these are extremes of opinion, so long as they can be urged in good faith, they must be met.

Perhaps the readiest brief answer to them is to be found in the fruitful applications of ecological knowledge to urgent problems of land use and management by such men as Phillips, Weaver, Tansley and many others, and by the Soil Conservation and Forest Services. Rather than dwell upon these, however, I wish to examine the structure of ecological thought to see where its own professors may have been at fault.

In most presentations of ecology one looks in vain for such names as Lavoisier, Ostwald, Sumner, Kropotkin and Henderson. Darwin is usually mentioned in connection with his work on pollination and competition, if at all. His equally important work on mutual aid, so unfortunately overlooked by Huxley, is often disregarded. Yet these men I have named are among those who are largely responsible for the only body of theory which, as I see it, can impart a fundamental unity to the tremendous bulk of ecological data which is being accumulated.

Briefly, Lavoisier demonstrated the orderly character of material interchange between organism and environment. With the development of thermodynamics the relation of this to energy was clarified. Ostwald stated explicitly that all life and living communities were part of the cycle of solar energy, elaborations of available free energy. Henderson studied the environment, analyzing it in terms of material and the energy cycle and showing its ultimately controlling character. From the physical or environmental side these men established what Darwin had proved from the biological side—that life and environment had to be considered together. Sumner I have mentioned because of his theory of folkways, since brilliantly elaborated into the concept of human culture forms. It is these forms which, emerging from human behavior patterns, largely determine human relations to the environment.

More recently other workers have invited attention to the fact that the interrelationships with which ecology deals involve systems of dynamic processes whose effects are genetic. These systems appear to exemplify principles of equilibrium which are universal. The problems of ecology have extension and continuity in time as well as space.

It is not my wish, in thus indicating a structure of basic theory, to detract one iota from the importance of the conventional lineage of ecological thought. Humboldt, Schouw, DeCandolle, Haeckel, Warming, Schimper and their successors shine as brilliantly as before. Indeed their work becomes more luminous as we insist that it deals with organized elaborations of the energy and material cycle.

Nor do I wish to imply that ecologists do not increasingly understand this fact. I am talking about what gets into their teaching and their apologetics. As a matter of fact, Adams[6] has sketched an outline of fundamental ecological theory. Transeau has successfully developed the idea of an energy budget for the landscape in his "Textbook of Botany" (1940). In related fields the soils students Jenny and Nikiforoff,[7] whose viewpoint is essentially ecological, have a clear conception of biological energetics. The posthumous paper of Raymond L. Lindeman in the October, 1942, issue of *Ecology*, in which the nutrient dynamics of aquatic habitats are developed, is a further case in point.

To my mind such considerations dispose of any charge that ecology is either amorphous or superficial. It should be neither. It should be, like the higher phases of mathematics, a viewpoint and an instrument which enables us to get behind what is behind, to determine the larger relationships in nature and guide the resolutions of their factors by whatever analysis may be necessary.

In the early phases of any science, men must grope their way. This is not a tidy business, particularly by

[6] C. C. Adams, *Ecology*, 16: 316–335, 1935.

[7] *Cf.* C. C. Nikiforoff, *Sci. Monthly*, 52: 5, 422–429, 1941.

comparison with subjects secure in a long tradition of disciplined and critical procedure. It must be admitted, too, that all ecologists have not dealt with important problems, nor held themselves to the standards of rigor which were possible.

In this connection, the literature dealing with the North American grasslands is instructive. It can be fairly described as a century of guessing, more or less shrewd, by men who were often highly competent in fields other than ecology. In the end—and in a surprisingly brief time—the fundamental rôle of available moisture was *demonstrated* by *ecologists*.

Not everyone who sayeth Lord, Lord, hath known the Name. There are still courses in "ecology" which resemble the regurgitations of a none-too-powerful vacuum sweeper. Yet it is fair to say that editorial boards of ecologists are as exacting today as they need be.

I am indebted to Professor Dunn for the reminder that biology often attracts individuals who from temperament or experience avoid the quantitative problems of science. As he puts it, "at the opposite end of the spectrum from the mathematical, physical and chemical (practicioners) of biology are the naturalists—taxonomists, ecologists, morphologists, etc." This is true. The impulse to do scientific work is itself an artistic, intuitive thing. The feeling for the significance of form is strong in some men, just as others are preoccupied with quantity.

That either viewpoint has any intrinsic virtue above the other may be doubted. In science, at least, each has to be judged by its fitness to the end in view. Ecology has today reached the point where increasing use is being made of the quantitative procedures. But the important consideration seems to me to be that the good scientist will follow his trail and develop his methods as he needs them. In my opinion the avoidance of quantitative work, if deliberate, is more often due to mental hazard than to actual incapacity.

The late William Bateson would not be accused of any lack of appreciation for quantitative work. Yet he told

me that he had been given up as a bad job by his mathematics instructors, and was handicapped all of his life by his ineptitude in that field. He returned the compliment done him by his teachers by saying that, if the subject had been presented by them as it is by their successors at Cambridge today, it would have aroused his highest enthusiasm. That he could have mastered it, no one familiar with his energy and penetrating intelligence can doubt.

I can not admit the argument that we have no business working at relationships in the natural environment until we know all there is to know about the anatomy, physiology and taxonomy of every organism that lives, and all there is to know about atmosphere and soil. I can not admit that the influence upon a community of lessened moisture supply is any less fundamental a fact than the physics of absorption or that the discovery of mutual aid within a species is a lower order of knowledge than the discovery of the neuromuscular behavior back of it. We need both kinds of knowledge and the mutual perspective they can supply.

What has all this to do with my topic? I have said that technically every student of the natural sciences is a naturalist, but that more and more of them reject the title. I have tried to show that Darwin considered himself a naturalist, and that the essence of his approach was the study of living organisms in their natural environment. I have tried to show that this approach is still a valid scientific procedure, which, under the designation of ecology, has a content and a possibility of organization that is intellectually respectable.

I should like to add that we are in the midst of a war of unprecedented tragedy and proportion and that this war is of itself a symptom of ecological maladjustment. I venture the opinion that until mankind looks upon its differences as arising from faulty adjustment within and among the communities of men and between those communities and their natural environment, there will be no

peace in any real sense. For peace is not the breathing space between wars. It is the orderly adjustment of men to the world they live in, containing in its structure the implicit guarantee of continued order. This I submit is fundamentally an ecological problem. In saying this, I do not minimize what may be termed the spiritual aspects involved, for they must work themselves out in material relationships.

The ecologist, more than any other worker in biology, continues the tradition of the naturalist as exemplified by Charles Darwin. Whether he is content to accept the designation of naturalist is not important. A definition is, after all, merely an invitation to accept a term in a certain, defined sense. I should like to invite him, since the term is already in practice restricted from its classical meaning, to consider himself a naturalist. No one can compel him to do so.

But I should further like to invite the American Society of Naturalists to extend to him, whatever he may choose to call himself, the same encouragement and active assistance which has, in the past four decades, wrought such magic within the "grand and almost untrodden field of inquiry . . . on . . . variation."

CHONDRODYSTROPHY IN RHODE ISLAND REDS[1]

DR. F. A. HAYS

During the hatching season of 1943 from March 7 to April 11 a type of chick abnormality appeared exclusively in the offspring from one mating pen. This was an inbred mating consisting of a cockerel mated to two of his full sisters and eight of his half sisters. This was the first inbred mating in this line of birds and previous to this generation care had been taken to avoid related matings.

Seven of the ten females, including the two full sisters, produced chicks with the abnormality, the total being 172 normal to 54 abnormal. If both parents were heterozygous for a single recessive gene producing the character the expectation would be 169.5 normal to 56.5 abnormal. This was a remarkably close fit to a 3 to 1 ratio and no single family deviated further than $2\frac{1}{2}$ to 1 or 4 to 1 from expectation.

This abnormality behaved as a lethal when present in homozygous condition and had a lethal effect even in the heterozygous individuals, as will be shown later.

Table 1 presents the complete hatching record of this pen. It will be noted that a considerable number of the embryonic deaths from the seven hens at 18 days were probably produced by the abnormality. When the eggs of these hens were taken from the incubator on the 22nd day 14 embryos were normal and 28 showed the abnormality.

Of the chicks that actually hatched from these seven hens, 140 were normal and 16 had the abnormality. An attempt was made to raise 12 of these abnormal chicks, but none survived longer than 7 days. The abnormal chicks could only crawl about on their abdomen and they were unable to open their beaks properly to take food and drink. With hand feeding on milk the largest survival period was 7 days.

[1] Contribution No. 498 from the Massachusetts Agricultural Experiment Station.

TABLE 1

HIGH MORTALITY LINE—HATCHING DATES MARCH 7 TO APRIL 11

Bird	Eggs Set: Total	Fert.	Dead before 5 days	Died about 18th day: Normal	Died about 18th day: Short	Alive or dead in shell at full term: Normal	Alive or dead in shell at full term: Short	Hatched: Normal	Hatched: Short	Totals: Normal	Totals: Short
W 160	35	33	9	6	3	2	3	9	1	17	7
W 184	38	35	1	5	0	1	0	28	0	34	0
W 228*	36	33	2	0	4	2	4	21	0	23	8
W 229*	35	33	0	4	0	3	7	18	1	25	8
W 753	39	37	0	2	1	2	3	26	3	30	7
W 1332	34	31	0	2	1	0	3	23	2	25	6
W 1334	39	37	3	4	0	4	0	26	0	34	0
W 1838	37	37	2	1	1	2	2	23	6	26	9
W 1839	34	30	3	3	0	1	0	23	0	27	0
W 1873	37	35	0	3	0	3	6	20	3	26	9
								From 7 hens Obtained		172	54
								Expected		169.5	56.5

* Full brother-sister mating.

EMBRYONIC AND POST-EMBRYONIC MORTALITY

The mortality records of the chicks from the seven hens in which the abnormality appeared may be compared with the mortality record of the chicks from the three hens where chicks did not show the abnormality. These data are presented in Table 2.

Embryonic mortality was obtained by dividing the number of fertile eggs into the total number of dead embryos at the end of the incubation period. Live chicks

TABLE 2

EMBRYONIC AND POST-EMBRYONIC MORTALITY IN CHICKS

Lethal hens	Embryonic mortality to hatching Per cent.	Mortality from hatching to 6 months Per cent.
W 160	63.6	55.5
W 228	33.3	61.1
W 229	30.3	50.0
W 753	10.8	65.4
W 1332	16.1	62.5
W 1838	13.5	56.0
W 1873	31.4	40.9
Mean	28.4	55.9
Control hens		
W 184	17.1	39.3
W 1334	18.9	23.1
W 1839	23.3	47.8
Mean	19.8	36.7

that failed to emerge were not included in the calculations. The mean embryonic mortality for the lethal group was 28.4 per cent. compared with 19.8 per cent. for the control group.

Post-embryonic mortality in chicks was calculated for the first six months of life. This calculation was made by dividing the number of chicks banded, which includes only 8 of the 16 abnormal chicks, into the number dying in a six-month period. The mean mortality in the lethal group was 55.9 per cent. compared with 36.7 per cent. in the control group.

These data indicate that chick mortality was significantly greater for the mothers that carried the abnormality gene than for those lacking the gene. This applies both in the embryonic and post-embryonic stages.

CHARACTER OF THE ABNORMALITY

This abnormality was observed for the first time in 1943 in a line of Rhode Island Reds being bred for high mortality in a cooperative project with the Regional Poultry Research Laboratory of East Lansing, Michigan. To produce this generation one cockerel was mated to two of his full sisters and to eight of his half-sisters. Previous to this time related matings had been avoided. All parents appeared to be physically normal.

The morphological characters exhibited by the chicks having the abnormality were very uniform. The head was wide and flat with both mandibles greatly shortened to produce very blunt beaks which did not open readily to take food or water. The shape of the beak was normal, except for its extreme shortness. Upper and lower beaks appeared to meet normally and no evidence of the so-called "parrot beak" was observed.

Long bones of both the upper and lower limbs appeared to be much shortened with some thickening in the humerus and ulna and extreme thickening in the tarsometatarsus. The femur was very crumbly and lacked a complete and distinct periosteum. All leg bones were straight. There

TABLE 3

LENGTH OF LONG BONES IN CENTIMETERS

	Normal (Landauer)	Abnormal (Mass.)
Femur	1.85	1.40
Tibia	2.61	1.85
Tarsometatarsus	1.99	1.15
Humerus	1.36	1.25
Ulna	1.28	.90

was no evidence of curvature in the tibia or of abnormal position of the lower limbs. The legs were so short that the hatched chicks were forced to struggle about on their abdomen and they moved around very little. In weight the chicks were normal but there was evidence of large yolk sacs as shown by distended abdomens.

In Table 3 are presented measurements taken on some of our abnormal chicks together with the normal reported by Landauer (1941).

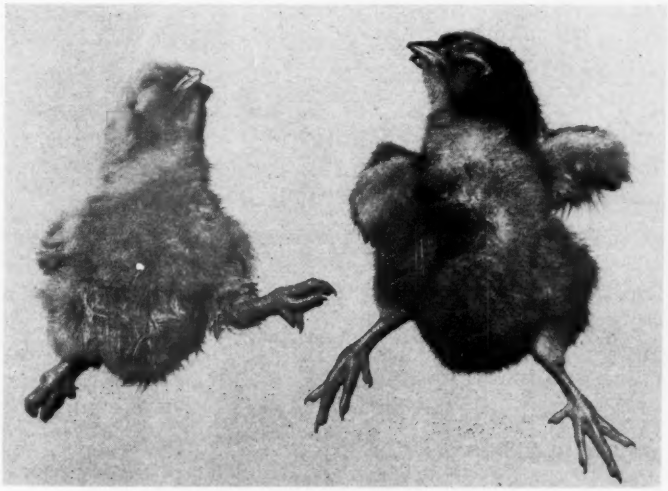

FIG. 1. Normal and abnormal chicks at hatching.—Mass Agr. Exp. Station.

DISCUSSION

The abnormality reported here does not appear to be the same as that reported first by Dunn (1923, 1927) and

studied later by Landauer and Dunn (1926), Hutt (1929), Munro (1932), Upp (1934), Landauer (1936), Lyons and Insko (1937), Lamoreaux (1942) and Asmundson (1942).

The abnormality described here has several distinctive features.

(1) It is characterized by great uniformity in its effects.

(2) Many of the homozygous chicks hatch normally.

(3) It greatly shortens the long bones of both upper and lower limbs but the bones are straight.

(4) The beak is very short but the upper and lower members are properly proportioned.

(5) Size of chick is not greatly reduced.

(6) Carrier parents give an extremely close approach to a three to one ratio.

From the effects produced on the embryos and chicks, it seems probable that the condition is due to faulty calcium metabolism and this may justify the use of the term chondrodystrophy. Further study is being given to this abnormality.

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A POSSIBLE FUNCTION OF VITAMIN K IN PLANTS

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I. INTRODUCTION

THE importance of vitamin K in the clinical treatment of unnatural bleeding has encouraged physiologists and biochemists to engage in numerous studies of the effects of this vitamin on the physiology of animals. Already, an extensive bibliography has developed (Merck, 1940, 1941a, 1941b, 1941c). Even a list of reviews of the literature is impressive.

Vitamin K is widely distributed in plants. Dam and Glavind (1938) found that green tissues contained the highest concentration. Grasses and alfalfa leaves were reported by Cravens, Randle, Elvehjem and Halpin (1941) to be particularly rich sources.

Despite the enormous literature describing the function of vitamin K in animals, there has been no attempt to define its significance in plants. Students have been so involved in the study of the vitamin requirements of animals that many have come to believe, at least by inference, that the chief function of vitamins in plants is to prevent vitamin deficiency diseases in animals and that the study of vitamin physiology is synonymous with deficiency diseases in animals. If we are to discover the fundamental activities of vitamins, we must study their reactions in the cells which produce them or require them. In other words, the "*cellular*" physiology of the vitamins, in plants as well as in animals, should be regarded as at least equally as important as their deficiency symptoms in animals, even though it may be many years before these studies can be completely related to each other.

The progress of the study of cellular physiology has been greatly aided by the many similarities between the behavior of animal and plant cells. In fact, it is cause

for constant wonder, how closely the physiologies of plant and animal cells resemble each other. For example, the reaction of enzymes, the utilization of oxygen and the transfer of hydrogen in the respiratory processes are identical or nearly so. Many examples could be listed, but it is necessary only to remind the reader that these similarities exist. The purpose of the present paper is to present a theoretical basis for a possible function of vitamin K in plant cells. The argument is based on certain analogies with blood clotting in animals, the formation of limiting protoplasmic membranes in both plants and animals, and vacuolization in plants. A brief discussion of these phenomena is necessary to indicate their bearing on the problem.

II. DISCUSSION

Blood clotting: Although the process of blood clotting is not yet understood in all its details, the following three stages are generally recognized. In the first, the prothrombin-heparin complex reacts with the cephalin freed by the disintegrating platelets to form prothrombin and cephalo-heparin. In the second, prothrombin forms thrombin by a reaction which involves free calcium ions. Ferguson (1938) has described the quantitative relation of calcium and cephalin to this reaction. The third reaction occurs between thrombin and fibrinogen to form fibrin. Calcium is not required for this reaction. The total process may be summarized as follows:

(1) (Prothrombin-heparin) + cephalin → prothrombin + (cephalo-heparin)
(2) Prothrombin + Ca → thrombin
(3) Thrombin + fibrinogen → fibrin

Serum which exudes from freshly clotted blood causes clotting of fresh blood in the absence of calcium ions by virtue of the thrombin which it contains.

Precipitation membranes: Protoplasm is frequently described as a colloidal system dispersed in an aqueous medium but yet immiscible with water. This immiscibility is generally held to depend on a morphologically dis-

tinct membrane. Many prominent authorities have stated that ruptured protoplasm has the power to form a new membrane over the freshly exposed surfaces. The first significant observations were reported by Naegeli (1855), who observed the phenomenon in cytoplasm squeezed from the cells of *Chara*, grape and other fruits. De Bary (1859) described a similar phenomenon in the naked cells of slime molds. Strasburger (1876) studied *Vaucheria sessils;* Klein (1872) *Pilobolus;* Van Tieghem (1875) the Mucorineae; Pfeffer the root hairs of *Hydrocharis* (1877) and slime molds (1890); Sachs (1882) and Prowazek *Vaucheria;* Stübel (1908) *Nitella;* Seifriz (1921) *Rhiopus, Fucus* eggs and *Iris* pollen tubes; Nichols (1922) *Vaucheria, Cladophora, Chara* and *Nitella;* and Lepeschkin (1926) *Bryopsis.* The eggs of many invertebrates also formed a similar membrane when ruptured. Heilbrunn (1928) reviews the data from the eggs of *Stentor, Arbacia* and *Echinarachnius.*

So many respected authors have described the ability of ruptured protoplasm to maintain its morphological identity in water that some writers assume that this is one of its fundamental properties. Yet Dujardin (1838) early in the nineteenth century had observed that not all protoplasm behaved in this way. The protozoans which he studied sometimes dissolved in water when the cells were crushed. At other times, he followed in the field of the microscope the visible formation of a surface membrane when the cells were ruptured. Evidently immiscibility with water is not an inherent quality of protoplasm, but depends on the variable ability of the protoplasm to form a membrane over the exposed surfaces.

Heilbrunn (1927, 1928) pointed out that the formation of the membrane was independent of adsorption phenomenon because adsorption could not occur until some kind of boundary had been established, because low temperatures which favor adsorption retarted membrane formation and because the membrane did not form in the absence of free calcium ions. Eggs of *Stentor, Arbacia*

and *Echinarachnius* were unable to form a precipitation membrane unless calcium ions were present. Strontium could replace calcium, but magnesium could not. Eggs crushed in solutions of sodium or other positive ions were unable to form a protective membrane. Chambers and Reznikoff (1926) found that amoeba quickly repaired tears in their surface membrane if they were in a dilute solution of calcium chloride, but were unable to do so in solutions of sodium chloride. Extracts of broken egg masses permitted surface precipitation by ruptured protoplasm in the absence of calcium. The presence of pigment granules also was found to be essential.

The stages in the formation of the precipitation membrane of invertebrate eggs were postulated by Heilbrunn (1928) as follows:

(1) Ca + pigment granules → ovothrombin
(2) Ovothrombin + protein → membrane

Since the ovothrombin of invertebrate eggs corresponds to the thrombin of the blood, Heilbrunn suggested that the term "cytothrombin" be used when the general reaction is considered.

The generality of this phenomenon for plant as well as for animal protoplasm is evidenced by the fact that Heilbrunn (1928) also found that extracts from crushed plant cells could hasten the coagulation of blood, presumably because the cytothrombin formed by the reaction of calcium ions with a protein during the crushing process could function as thrombin.

Vacuolization: According to Heilbrunn (1928) the formation of the precipitation membrane is initiated by the appearance of free calcium ions in the protoplasm. Internal precipitation of the protoplasm is prevented by the adsorption of the calcium ions on cellular colloids. Heilbrunn (1928) believes that any factor which releases calcium from internal colloidal surfaces will lead to the formation of localized, internal precipitation membranes. When this occurs, osmotic activities of the membrane result in vacuole formation. While this theory offers an

explanation of that type of vacuolization involved in the formation of many small vacuoles, its application to the formation of the single large vacuole typical of many plant cells is uncertain. It is particularly significant in this connection that the figures by Sachs (1882) of ruptured *Vaucheria* cells show the formation of small vacuoles in the exuded part. It is not clear, however, why these internal precipitation membranes should be spherical, or at least shaped in such a manner that vacuoles appear as a result of their osmotic activity.

Cytolysis of the eggs of invertebrates, certain other types of animal cells and of plant cells may result if the processes of vacuolization proceeds far enough to cause the bursting and general disintegration of the protoplasm.

This theory of vacuolization is supported by the fact that physical as well as chemical agents which release calcium from colloidal surfaces cause the production of vacuoles and, in extreme cases, cytolysis. The agents known to affect both plant and animal cells in this way are distilled water, strong acids, strong alkalis, extreme cold, heat, electric currents, fat solvents, radium, x-rays and mechanical injury. It is interesting to note that this theory also accounts for the high viscosities of protoplasm obtained by Seifriz (1936) by microdissection. Any procedure as violent as manipulation with needles almost certainly would lead to the formation of internal precipitation membranes with a great increase in the viscosity of the mass.

Analogies between plant and animal protoplasm: The free calcium ions in the blood are unable to cause the formation of thrombin from prothrombin until cephalin has first removed the heparin from the prothrombin-heparin complex. Cephalin also occurs in plants and Harrow (1940) describes the ability of preparations from soybeans, cotton seeds and yeast to replace the cephalin from the platelets during the clotting process. It is not certain that a cyto-prothrombin-heparin complex exists in plant protoplasm, but the presence of cephalin sug-

gests that it might function in some preliminary reaction similar to that in blood clotting. Heilbrunn (1928), on the basis of the work of several authors, has described the close analogy between the processes of blood clotting in animals and membrane formation, vacuolization and certain types of cytolysis in plant and animal cells. These similarities may be summarized as follows:

(1) An early stage involves a reaction between free calcium ions and a protein (= prothrombin) to give cytothrombin (= thrombin, ovothrombin).

(2) This stage is furthered by factors which release calcium ions from colloidal surfaces.

(3) A later stage involves a reaction between cytothrombin and a protein (= fibrinogen, pigment granules) to give a precipitation membrane (= fibrin, cytoplasmic membrane, vacuole membrane).

(4) The necessity of the ionized calcium is eliminated by the presence of the extracts from cell masses containing cytothrombin (= fresh blood clots, crushed invertebrate eggs, crushed plant cells).

(5) Cytothrombin from plant and animal cells is more or less similar, since extracts of crushed plant cells hasten the clotting of blood.

III. Function of Vitamin K

It is now generally recognized that vitamin K is intimately concerned in the process of blood clotting. Elliott, Isaacs, and Ivy (1940) found that subcutaneous injection of this vitamin corrected the tendency to hemorrhage and shortened prothrombin time in rats. Cravens, Randle, Elvehjem and Halpin (1941) reported that the blood-clotting time of day-old chicks depended on the amount of vitamin K in the ration of the hen. A diet containing 2 per cent. dried alfalfa leaf or 1 per cent. of dried cereal grasses allowed an adequate intake of vitamin K by the hen. Schonheyder (1938) also reported the relationship between the plasma prothrombin and vitamin K for chickens. A diet free from vitamin K was shown by Stefanini (1940) to decrease the amount of prothrombin in rabbit blood. The use of vitamin K to shorten the clotting time of the blood of infants, by increasing the prothrombin has been described by Waddell (1939). Hogan and Johnson (1936) reported that vitamin K in extracts of alfalfa or of young cereal grasses in the diet

of guinea pigs lessened the number of young to die from hemorrhage at birth. The general clinical importance of vitamin K has been studied by many workers, and a large number of reviews of the literature have been published.

The wide distribution of this vitamin in plant cells suggests some fundamental significance in the physiological processes of plant cells. So specific is the relationship of vitamin K to the prothrombin level in blood that it has been called the "antihemorrhagic" vitamin. The close similarity between the process of blood clotting and the phenomena of membrane formation and vacuolization in plants suggests that it is not improbable that vitamin K is concerned with the formation of a "cyto-prothrombin" in plant cells which is a necessary precursor to the formation of precipitation membranes and vacuoles.

IV. Summary

The formation of precipitation membranes by plant protoplasm resembles the clotting of blood in the following respects: (1) In blood cephalin frees prothrombin from the prothrombin-heparin complex. Cephalin is found also in plant protoplasm where it may have a similar function. (2) Free calcium ions are necessary for the formation of a cytothrombin (= thrombin, ovothrombin) from a protoplasmic protein (= prothrombin). (3) Chemical and physical agents further this process by freeing calcium ions from colloidal surfaces within the protoplasm. (4) Cytothrombin reacts with a cellular protein (= fibrinogen, pigment granules) to give a precipitation membrane (= fibrin, cytoplasmic membrane, vacuole membrane). (5) The necessity of free calcium ions is eliminated by the presence of extracts of cell masses containing cytothrombin (= fresh blood clots, crushed invertebrate eggs, crushed plant cells). (6) Extracts of crushed plant cells hasten the clotting of blood.

The necessity for vitamin K in the formation of prothrombin in blood suggests that it may be concerned with

the formation of a "cyto-prothrombin" in plant protoplasm. This substance could be a precursor of the precipitation membranes which prevent the dissolution of plant protoplasm in water and also to permit the formation of vacuoles.

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THE MAINTENANCE OF VITALITY IN PURE LINES OF THE CILIATE *TILLINA MAGNA*[1]

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THE most extensive study made to date on the structure and life history of *Tillina magna* is that of Gregory (1909), who placed the ciliate in the order Holotrichida, suborder Trichostomina, family Chiliferidae. Gregory found her specimens in a laboratory jar containing a horse-manure infusion and suggested that the organism possibly might be a facultative parasite of the horse intestine. However, it is now generally agreed that while Gregory's order and suborder designations are correct, *Tillina* is actually a member of the Colpodidae, as Kahl (1931) and Turner (1937) have pointed out. Furthermore, there is no satisfactory evidence that *Tillina magna* may occur as a facultative parasite of the horse. It is unmentioned in Hsiung's monograph (1930) on the intestinal protozoa of the horse, and the records of its occurrence, while not at all plentiful, show that it is to be regarded exclusively as a freshwater ciliate.

Gruber (1879) established the genus and species, and described the method of division within a thin-walled cyst. His specimens came from a small aquarium into which dried mud from Vienna had been put. Evidently the mud contained dried protective or resting cysts. Ilowaisky (1921) found *Tillina magna* in freshwater pools in the vicinity of Saratov, though he described it as *Pseudocolpoda cochlearis cienkowskii,* and Bresslau (1922) found it in infusions made from meadow turf. I have taken it repeatedly in the past five years from tem-

[1] I am indebted to Dr. C. V. Taylor, professor of biology in Stanford University, for generously placing at my disposal the facilities of his laboratory during my tenure of a leave of absence on the Kenan Foundation of the University of North Carolina.

porary pools in a meadow near Chapel Hill, North Carolina. Following prolonged rains these pools yield active tillinas. In periods of summer drought when the pools disappear the bottom debris yields dried protective cysts which activate readily upon transfer to water. These specimens agree in all respects with Kahl's description (1931, p. 282) of *Tillina magna.*

Of the many observations made by Gregory on the general biology of *Tillina magna,* the following may be mentioned as having a special bearing on the present study. Reproduction occurs only by the formation of spherical division cysts, within which the parent organism undergoes usually 2 successive cell divisions. Upon the rupture of the thin cyst membrane the 4 offspring emerge as fully developed individuals, merely smaller than the parent. Under favorable conditions this process occurs once a day, and the 4 individuals so produced are counted as 2 generations. Thick-walled protective or resting cysts are also formed under certain conditions—chiefly adverse ones.

In her life history studies Gregory established 2 pure lines, each consisting of 4 sublines, which were maintained on horse-manure infusion in depression slides, since *Tillina* is a bacterial feeder. Both lines showed periodic fluctuations or rhythms in the reproductive rate, which Gregory considered to represent "periodic variations in the vitality of the protoplasm" and to be independent of environmental changes. As generations passed both lines showed a gradual decline in vitality which was expressed first in a progressive decrease in the rate of division and later in the death of the lines. The first line produced 210 generations in the 112 days of its life; the second, 548 generations in 405 days. Attempts to stimulate the declining lines by a variety of chemical and physical means were largely unavailing, and the conclusion was reached that in *Tillina* the passage of generations results in a gradual decrease in the vitality of the protoplasm. By what means, natural or artificial, this

inherent tendency toward decline and death may be offset was not made clear by Gregory.

Reference may be made to Calkins (1933, pp. 244–260) for a discussion of the problem of vitality in ciliates and for a critical evaluation of the results of a considerable number of studies that bear upon the problem.

The present study was begun in an attempt to answer the following questions. Can an entirely satisfactory and wholly reproducible culture method be devised for *Tillina magna?* Does *Tillina* under adequate and constant conditions of culture show periodic fluctuations in the rate of reproduction and suffer as generations pass a decrease in vitality that terminates in death?

The success of Taylor and his associates (e.g., Taylor and Strickland, 1938) in culturing *Colpoda duodenaria* on a suspension of the bacterium *Pseudomonas fluorescens* in a buffered, non-nutrient solution of inorganic salts of Na, Mg, K and Ca suggested the use of a similar procedure in culturing *Tillina*. Accordingly, a solution having a total salt content of 0.012 per cent. was prepared with Pyrex-distilled water and its pH value was adjusted to 6.8, following the directions given by Barker and Taylor (1931, p. 622). To each 5 cc of this solution was added a heaping loop of *Pseudomonas fluorescens,* which was grown on Difco nutrient agar. Unfortunately, the use of this medium for the growth of *Tillina* was disappointing, in that the animals instead of spiraling smoothly or feeding leisurely on the bottom—characteristic features of their normal behavior—would swim rapidly in small circles just beneath the surface film and on occasion would burst and disintegrate. That there was nothing essentially toxic or injurious to ciliates in the medium was shown by the fact that both *Paramecium caudatum* and a species of *Colpoda* could be grown in it with complete success. Many different concentrations of the salt medium and many modifications of the formula were tested, but in none did *Tillina* react normally and grow satisfactorily. Hence, the use of a completely re-

producible, non-nutrient medium with bacteria added was reluctantly abandoned, and out of expediency a culture medium made as follows was adopted. To 4 cc of the 0.012 per cent. salt medium of pH 6.8, one cc of 0.05 per cent. sterile lettuce infusion (prepared by boiling 0.1 gm powdered dried lettuce 5 minutes in 200 cc water) and the usual loop of bacteria were added. In this medium, which will be referred to merely as "lettuce medium," *Tillina* invariably reacted normally and flourished. I am unable to explain satisfactorily the lack of tolerance shown by *Tillina* for any of the inorganic solutions tested. The evidence indicates that *Tillina* lacks the capacity for adjustment to chemical and physical changes which certain other ciliates are known to possess, and this circumstance may account for the seeming rarity of *Tillina* in nature.

To obtain specimens for vitality studies resting cysts were transferred into fresh 0.05 per cent. lettuce infusion as a means of activation. These cysts were 7 weeks old and represented a wild population which had encysted in an old lettuce-infusion culture when the food supply became exhausted. Active individuals emerged from nearly all of the cysts after approximately 3 hours in the excysting infusion, and several of these were isolated in depression slides in lettuce medium. On the following day 2 pure lines (designated as A and B) each consisting of 4 sublines were established with the progeny of 2 of the excysted specimens. In this process each ciliate was isolated in 0.2 cc lettuce medium in a clean depression slide, and the slides were transferred immediately to moist chambers which were kept in a constant temperature oven at 21° C. The arrangement was such that the cultures received 8–12 hours of light each day, as they would in nature. On each succeeding day 4 of the progeny of each pure line were transferred to clean slides and fresh lettuce medium. Records were made daily of the number of divisions undergone by each subline in the preceding 24 hours, and from these the average daily

fission rate per line (A or B) was calculated. Thus the animals were grown under conditions of as high a degree of constancy as their somewhat refractory nature permitted, though it is recognized that the addition of lettuce infusion to the medium introduced a potential variable, particularly with reference to the bacterial flora. However, it is believed that the daily changes to fresh lettuce medium, the use of consistently clean glassware and the briefest possible exposure of the cultures to room air at the time of transfer so restricted the growth of contaminating bacteria that their presence was without significance.

The 2 lines were cultured for a period of 220 days, whereupon the experiment was discontinued. In this period Line A produced a total of 579 generations, and Line B, which had consistently a slightly lower division rate, 525 generations. Since the cultural histories of the 2 lines were essentially identical, only that of Line A will be considered in detail.

In Table 1 the average daily fission rates of the 4 sublines of Line A are averaged further for 10-day periods (column 2), and the total number of generations through each successive 10-day period is calculated (column 3). Examination of column 2 shows that the rate of reproduction was remarkably constant throughout the experiment, varying only from a minimum production of 25 generations (an average of 2.5 fissions per day) in the 8th, 13th and 21st periods to a maximum of 28 generations (2.8 fissions daily) in the 19th period. Since the lines produced an average of 2.63 generations daily throughout their life, these departures from the average, amounting at most to only 6.5 per cent. in the case of a production of 2.8 fissions, can scarcely be considered to have significance. In view of this fact, it is evident that the division rate was as high at the end of 220 days or 579 generations of culture as it was when the lines were established, and there was no evidence of a decline in vitality as measured by the division rate. Furthermore, under the constant

conditions of the experiment there was no indication of periodic fluctuations or rhythms in the reproductive rate.

It is well known that diminished vitality in ciliates may express itself not only in the division rate but in structural abnormalities and in a decrease in the size of the animals (Maupas, 1888). In the present study neither the active tillinas nor the division cysts showed any structural departures from the normal or any decrease in size

TABLE 1

SUMMARY OF RATE OF REPRODUCTION OF A PURE LINE OF *Tillina magna* UNDER CONSTANT AND ADEQUATE CONDITIONS OF CULTURE. NOTE THAT NO LOSS OF VITALITY AS MEASURED BY THE FISSION RATE OCCURRED, EVEN AFTER 579 GENERATIONS OF CULTURE.

Successive ten-day periods	Total average number generations for the period	Total average number generations to date
1	27.0	27.0
2	27.5	54.5
3	26.5	81.0
4	25.5	106.5
5	26.5	133.0
6	26.0	159.0
7	27.0	186.0
8	25.0	211.0
9	26.5	237.5
10	25.5	263.0
11	27.0	290.0
12	27.5	317.5
13	25.0	342.5
14	26.5	368.5
15	26.5	395.0
16	25.5	420.5
17	27.5	448.0
18	26.0	474.0
19	28.0	502.0
20	25.5	527.5
21	25.0	552.5
22	26.5	579.0

as generations passed. Ten active specimens of maximum size selected at random from Line A in the first 10-day period measured on the average 268 $\mu \times 183$ μ, and 10 division cysts had an average diameter of 205 μ. The dimensions of active specimens and cysts from later periods showed no significant departures from these measurements. For example, 10 division cysts from the 11th period had an average diameter of 198 μ, and 10 from the 22nd period, a diameter of 207 μ. These measurements furnish additional evidence of sustained vitality throughout the experiment.

Endomixis was never observed in the active specimens

of either line, nor did conjugation occur at any time among individuals of the lines or among their surplus progeny. Attempts to induce conjugation in small populations by increasing the temperature, varying the amount of the food, altering the pH and changing the salt content of the medium ended without exception in failure. As a matter of fact, conjugation has never been reported in *Tillina*.

Likewise, the spontaneous formation of protective cysts was never observed in the lines, though such cysts could be produced at any time by allowing the food supply to become exhausted. Unlike *Colpoda duodenaria* (Taylor and Strickland, 1938), washed tillinas could not be deprived of food and made to encyst reliably in any inorganic medium that was tried. Their behavior in such solutions, as has been stated, was never entirely normal and their fate was unpredictable. A tillina might burst soon after transfer or after many hours, it might swim continuously for 4 days and perish, or it might divide to form 2 offspring which might or might not encyst. On the contrary, surplus animals from the pure lines if left in lettuce medium could always be depended on to produce protective cysts after 2 or 3 days. That such cysts resulted from absence of food was readily demonstrated. If additional bacteria were put into the cultures at intervals over a period of several days, reproduction continued without the formation of resting cysts, until as many as 500 or 1000 active tillinas and division cysts were present in each of the small amounts (0.2 cc) of lettuce medium. Later these specimens formed protective cysts. Such cysts remained viable for 6 months or longer and never showed spontaneous activation, as do cysts of *Colpoda duodenaria* under certain conditions (Taylor and Strickland, 1938). The ability of the pure lines to produce normal resting cysts at any time is further evidence of sustained vitality in the lines, for Beers (1928) and Johnson and Evans (1939) in studies on *Didinium nasutum* and *Woodruffia metabolica*, respec-

tively, have shown that impaired ability to produce resting cysts is an accompaniment of lowered vitality, induced, however, in their studies by dietary inadequacies and not by the passage of generations.

The evidence adduced from the present study shows that in *Tillina magna* there is nothing in the nature of a definite life cycle embracing a period of high vitality followed by progressively diminishing vitality and death as generations pass. The history of a pure line in the laboratory or of a population in nature appears to be purely a function of the environment. Under favorable and adequate conditions of culture, *Tillina magna,* like *Didinium nasutum* (Beers, 1929) and *Woodruffia metabolica* (Johnson and Evans, 1939) appears to be capable of indefinite reproduction without loss of vitality and without recourse to endomixis, conjugation or to the production of resting cysts.

The decline in vitality and the rhythms observed by Gregory were undoubtedly the results of the variable and inadequate conditions under which cultures were maintained in the earlier years of pure-line investigations—conditions which have since been vastly improved by the utilization of constant temperature apparatus and by the employment of pure strains of bacteria. The temperature varied greatly in Gregory's experiments, as she herself points out (pp. 401 and 403), and both the nature and the number of bacteria available as food were quite uncontrolled. It is well known that changes in temperature regularly produce fluctuations in the rate of reproduction of infusoria, and that any failure to control the quality and the quantity of the food available to animals under investigation, whether protozoan or metazoan, constitutes without exception a potential experimental variable. Whatever may have been the factors involved in the decline observed by Gregory, the fact remains that under the conditions of culture maintained in the present investigation the lines of *Tillina* failed to exhibit either rhythms or diminution in vitality.

SUMMARY

Two pure lines of the freshwater ciliate *Tillina magna* were maintained in lettuce medium on the bacterium *Pseudomonas fluorescens* for 220 days. In this time they produced a total of 579 and 525 generations, respectively. Under the constant conditions of culture employed, rhythms in the reproductive rate were absent. Neither conjugation nor encystment was observed, and the formation of protective cysts occurred only in subcultures when the food supply became exhausted. When the lines were discontinued, after 220 days, the vitality of the animals as measured by the fission rate was unimpaired by the passage of generations, and their size and structure were normal. The results indicate that in *Tillina magna* there is nothing in the nature of an intrinsic life cycle embracing in succession states of high vitality, decline and death.

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REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

In this section reviews and notices are given of current publications on general biology and of specialized works which have an important bearing in this general field. Emphasis is given to books and major articles which fall within the special scope of The American Naturalist, in that they deal with the factors of organic evolution.

Reviews and Comments are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

Man's Unknown Ancestors The Story of Prehistoric Man. By Raymond W. Murray. Milwaukee: Bruce Publishing Co., 1943: i–xiv, 1–384, 36 pls. $4.25.

The Stage for this semipopular recital of prehistory was set by swift-moving advances, during the pre-holocaust decade, in our knowledge of human evolution. The interlude of the war has permitted an appraisal of the great mass of new evidence, has made possible a collation of the diverse interpretations, and has allowed a book on the lineage of man to remain up-to-date during its printing. The non-specialist is given résumés of Weidenreich's epochal work in China and of von Koenigswald's in Java, on the evolving semi-humans generally known as *Sinanthropus* and *Pithecanthropus* and on the more truly human kinds which followed in those countries; of the enlightening new discoveries concerning different races of Neanderthal men; and of other researches on prehistoric men in Africa, Eurasia and the Americas. The author tentatively adopts but does not consistently follow Weidenreich's new synthetic classification of fossil men into three divisions: division 1, *Homo erectus,* with two subspecies—*H. e. javanensis* (preferably *H. e. erectus,* to accord with the International Rules of Zoological Nomenclature), which is a new alignment of *Pithecanthropus erectus,* and *H. e. pekinensis,* in place of *Sinanthropus pekinensis;* division 2, *Homo neanderthalensis,* with *soloensis* of Java and *rhodesiensis* of South Africa as sub-

species; and division 3, *Homo sapiens*. The family tree of man is pictured as extensively branched, with a wide evolutionary range in existence at each time level.

Professor Murray's treatment strikes me as thorough, conservative and judicious. I arrive at this appraisal chiefly from his account of the discoveries of early man in America, particularly in the desert regions, since this is the only field of prehistory which I have made any attempt to follow. He states, but not dogmatically, that the evidence strongly confirms the views of certain workers that man lived in North America, in company with extinct mammals, during the early postglacial period, approximately 10,000 to 25,000 years ago, and may have existed on the continent during glacial and interglacial time.

To a limited degree throughout the book, and extensively in the final chapter, the author engages in discussions of "Prehistory and Religion." Much of this argumentation is essentially a defense of the Catholic position. The conflicts between prehistory and religion and between evolution and religion are pictured as discordances between science and Fundamental Protestantism. Catholic scholars are indicated as willing to allow or accept evolution, even of man's body and brain (but not of his soul) and as free to interpret the Biblical account of Genesis as figurative (but never as in substantial error, and never as in any way contrary to the limits defined in Rome). Such discussions will strike many readers as unpleasantly out of place, definitely anachronistic. However, the only interpretations in the book which seem flavored by religious views are the attempts made now and then to line up anthropological findings with the Biblical legends. Let us remember that the vision of many potential readers of "Man's Unknown Ancestors" is still blindfolded by religious myths. Professor Murray's book may open their view to the glorious horizon of science.

Man, Real and Ideal Observations and Reflections on Man's Nature, Development, and Destiny. By EDWIN GRANT CONKLIN. New York: Charles Scribner's Sons, 1943: i–xvii, 1–247. $2.50.

A DEEP-THINKING biologist gives in this readable little book a fine philosophy of human biology. He strikes a compromise—at times may seem to waver—between mechanism and vitalism, but since his mechanism is thoroughly grounded in rich biological experience and since his concepts of vitalism are very broad, his pen picture of life in general and of human life in particular is a very logical one. He reaches compromise more by addition than by averaging, for he accepts most of the fundamental facts and interpretations of mechanistic biology, but builds thereon a philosophy of creative synthesis. Similarly, instead of taking sides or trying to straddle the line between science and art, or between science and religion, or between science and ethics, or between the intellectual and the spiritual, or between the real man and the ideal man, he accepts both elements in each contrast.

The first part of the book, dealing with "The Human Species," contains much biological wisdom. For example, the author stresses the point that "individually acquired adaptations are fundamentally similar to normally inherited ones, and it is difficult to resist the conclusion that the two must be results of similar causes." The parallelisms between mutations and responses are also pointed out. The conviction is reached that "man is the last, best hope of future evolutionary progress in body, mind, and society." "The lesson of evolution is full of hope for the future, a real 'gospel' to a distracted world."

In the relatively extensive treatment of the "Development of the Individual" (Part II) the author brings out his summational philosophy of mechanism and creative synthesis: "Mechanism is universal, but so also is finalism . . . These two aspects of life are not antagonistic, but complementary."

The third part of the book, "The Real and the Ideal" starts with a very able and convincing defense of science, continues with a discussion of the role of science and of ethics and religion in human life, and ends with an essentially non-biological discussion of current problems of war, peace and international politics. The final conclusions, however, are that:

> The long course of organic evolution justifies faith in further progress . . . There has been no permanent retreat in the evolution of intellect, reason, and ethics. These are the perfecting principles in human life and evolution . . . We are today only children in the morning of time, and before us lie the countless centuries and millenia of man's vast future.

Genes and the Man. By BENTLEY GLASS. New York: Bureau of Publications, Teachers College, Columbia University, 1943: i–xii, 1–386, figs. 1–108. $3.50.

"THIS VOLUME," the author tells us, "has been prepared to indicate a new outlook, not to present genetics or cytology, or embryology, or physiology, or even a summary of all of them, but rather to describe the operation and interaction of those factors which make the physical man, insofar as we know them or can reason about them today." "Throughout the realm of science," he wisely observes, "the narrow, rigid boundaries of specialized fields of subject matter are at last breaking down. The boundary between genetics and cytology has already disappeared, and it is now evident that embryology and physiology are beginning to enter the amalgam. As yet, however, the trend is apparent only in the more technical studies." Professor Glass has therefore essayed an elementary synthesis of the sciences which contribute to our understanding of the ontogeny of man. While realizing that his experiment in this direction has met with marked success, many will wonder why he left out of his "amalgam" all but the most incidental treatment of evolutionary biology (beyond the field of genetics). He attempts to answer, What makes man?, but fails to consider, What made man? Social evolution is also neglected, as in the final conclusion that our genes are all that survive us.

I will not attempt an appraisal of the pedagogical advantages or shortcomings of "Genes and the Man," beyond observing that there is evident no regular gradation from known to unknown or from simple to complex. The presentation throughout is a mosaic of the elementary and the technical. Perhaps this is as it should be.

The scope of treatment involves the danger of portraying man as an isolated phenomenon. This peril, however, is largely avoided by frequent comparisons of the structures and functions of other organisms with those of adult man, or with those of the corresponding stage in embryonic development.

The work is technically sound, the diction good and the diagrams clear-cut. The half-tones, however, are pepless. *C'est la guerre*, perhaps.

Naturalist at Large. By THOMAS BARBOUR. Boston: Little, Brown & Co., An American Monthly Press Book, 1943: i–xii, 1–314, 23 pls. $3.50.

BRIMFUL of grand personality, this literary treat gives us, in his own words, much as he would tell them during lunch in his famous Eateria or at smoke-time on the back stoop of M.C.Z., the life story of Thomas Barbour, fascinating incidents from his almost endless travels, keen appraisals of his acquaintances, and a little of his biological philosophy. Tom Barbour's heart grew out of proportion to the frame that holds it, and that, in the language of the street, "is something." He is not only an outstanding investigator, administrator and counselor, but also the kindliest and wisest *patrón* of naturalists and of natural history institutions. In some of his many effective acts he takes just pride, for instance in the development of Barro Colorado Laboratory in the Canal Zone and of the Harvard Garden at Soledad in Cuba, and in the bringing of new light, figuratively as well as literally, into America's greatest university museum. On other accomplishments he maintains a modest silence. A host of younger men to whom he has given a strong hand of

fatherly help will do a lot of between-line reading. There are few, in the biological sphere, to whom "so many owe so much"; and, we suspect, there are few who have gained more full-hearted satisfaction out of doing so much for so many.

Here and there throughout the book and particularly in the appended "For Zoographers Only," Dr. Barbour gives us some of the conclusions which he has reached as results of his rich experience in the field of zoogeography. He is an advocate of the land-bridge origin of the faunas and floras of the West Indian and East Indian islands.

In "The Tests of Evolution" he stresses the unknown and possibly unknowable why's of organic evolution. For him there remains much room for religious faith. With approval he quotes Regan in circumscribing the role of mutation in speciation, and Cope in postulating a " 'super-abundant growth force'—growth in a particular direction until it becomes fatal." Some of us who have had the privilege of knowing Dr. Barbour personally (and know him now much better after the reading of his grand book), would like to take friendly issue with him in person on some of these points—or to talk with him on any subject of his own choice; he is always interesting and inspiring.

Physiological Regulations. By EDWARD F. ADOLPH. Lancaster, Pa.: The Jaques Cattell Press, 1943: i–xvi, 1–502, figs. 1–186. $7.50.

I OPENED this book with the expectation of finding therein a detailed contribution on progressive evolution, for I had recently been deeply impressed by Julian Huxley's view that greater independence of the environment, along with greater control over the environment, is a main criterion of biological progress. In this respect I was abruptly disappointed. Adolph shies from any considerations other than those of quantitative data which may be tabulated or graphed. He tells us:

> Like other students of biology, I was repeatedly told that regulations were important. What they were and how they operated was far from apparent.

Gradually they acquired meaning, not as inferences from metaphysics, but as hazy inductions from biological experience. More recently I observed data concerning balances, variabilities, recoveries, and behaviors that manifest a common bearing upon the maintenance of properties. Bit by bit I have come to realize that this pattern of maintenance is probably what my preceptors were talking about. But, as a result of my backwardness I have an unforeseen advantage over them, for I build my abstractions about equilibration diagrams and frequency diagrams, while they used words. My concept is in quantitative and dimensional form, theirs was, I infer, less definitely founded.

Despite its size this volume is not a general treatise on physiological regulations. It is essentially a report on the author's extensive experiments. Though the discussion of regulations in the water relations of animals occupies about 300 pages, there is no adequate phylogenetic analysis of water-regulating mechanisms; hardly a mention, even, of the extended researches of Homer Smith, E. K. Marshall and others on the very interesting methods by which different groups of fishes control the amount of water in their systems.

I take it that "Physiological Regulations" is a tremendously important addition to the literature of physiology, but its contribution to evolutionary thought is limited to the extensive data which may be utilized by others, less adverse to philosophical interpretation.

Studies in the Life History of the Song Sparrow II The Behavior of the Song Sparrow and Other Passerines. By MARGARET MORSE NICE. Trans. Linn. Soc. N. Y., 4, 1943: i–viii, 1–328, 1 pl., figs. 1–6. $2.00.

WITH the publication of Part II of her 15-year study Mrs. Nice has made the Song Sparrow (*Melospiza melodia*) of the northeastern United States perhaps the most thoroughly known wild bird in the world. Part I dealt with matters of vital statistics—population and reproduction; Part II treats the behavior of the Song Sparrow and other passerines. It is, in fact, practically a monograph on bird behavior (about 420 species of birds are referred to).

Mrs. Nice's study is a splendid example of a comprehensive, well-planned campaign of field investigation

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carried through a number of consecutive seasons, then thoroughly correlated with the world scientific literature and carefully prepared for publication in the most usable form. Each chapter is well organized and fully documented and concludes with a brief summary. The volume has an extensive bibliography and good indices. Unfortunately the prospective reader must be warned that the volume contains a considerable number of minor errors, not all of which can be attributed to the printer.

There is a wonderful opportunity now for bird students to compare with this account their findings on the characteristics of other members of that great complex of Song Sparrow subspecies that range from the pallid little *saltonis* of the southwest to the blackish *rufina* of southern Alaska and the giant race *sanaka* of the Aleutian Islands. In fact, one of the important contributions of this work will prove to be its tremendously stimulating effect on ornithological research of many kinds.

The American Ornithologists' Union expressed the opinion of ornithologists generally when it awarded Mrs. Nice the Brewster Medal in 1942 in recognition of this study as the "most important work relating to the birds of the Western Hemisphere."

JOSSELYN VAN TYNE

SHORTER ARTICLES AND DISCUSSION

VARIATION IN PETAL NUMBER IN THE BLOODROOT, SANGUINARIA CANADENSIS

For some years in our course in genetics at Wooster we have carried on studies of variation in natural populations of certain plant species. The spring beauty, *Claytonia virginica*, has furnished unusually favorable material for a study of microevolution (Spencer, 1942). We herewith present material on variation in petal number in the bloodroot, *Sanguinaria canadensis*, collected biennially since 1926. Unfortunately the collection records for two of these years have been lost. One other year the short flowering period passed without records being taken. To the many students in his genetics classes who have aided in this project, the author is indebted.

Sanguinaria, belonging to the poppy family, is described in Gray's Manual as follows:

> Sepals 2. Petals 8–12, spatulate-oblong. Stamens about 24. Style short; stigma 2-grooved. Pod ellipsoid or fusiform, turgid, 1-celled, 2-valved. Seeds with a large crest.—Low perennial; its thick prostrate rootstocks sending up in earliest spring a palmate-lobed leaf with 1-flowered scape. Flowers white, handsome, the bud erect, the petals not crumpled.—Open rich woods; common. Apr., May.

The petal number is sufficiently large to give a workable morphogenic series and sufficiently small to make possible the securing of extensive data with reasonable expenditure of effort. In our latitude the plant flowers in late April and early May. The flowering period in a given locale is short, a week to 10 days. During this period there is a peak lasting for about 3 or 4 days, and it is during this peak that data have been secured. In northeastern Ohio populations of this species are quite common but discontinuous. These may consist of isolated patches of a few hundred plants scattered over an area of an acre or less to large colonies a half mile or more in length. The latter are broken up into concentrated subpopulations where plants are very numerous. The distribution is definitely related to the drainage systems, with colonies occupying the sloping, open-wooded banks along stream valleys. Thus many colonies average 20 to 100 yards in width and extend for considerable distances along these

banks. Where the slope is more gradual the colony spreads out correspondingly.

We have made collections principally from two populations. The Overton Road population occupies a wide sloping meadow and open woodland at the fork between the Killbuck and Little Killbuck valleys in Wayne County, Ohio. This population covers an area roughly one-third mile long by one-fourth mile wide. The Little Apple Creek colony, the smaller of the two, stretches for about one-half mile along the steep banks on the eastern side of the valley, and varies in width from 20 to 100 yards, with tongues running up the ravines leading into the valley floor. These two colonies are approximately 4 miles apart.

Data are collected as follows: During the peak of the flowering period a group of workers, each with pencil and card, works through a colony, pulling off flowers, and counting and recording petal number. In this way the same flower can not be recorded twice. The group of workers varies from 5 to 20, and by working through the area covered by a population probably secures a better sample than one worker, even though he collected the same amount of data. By collecting on one day no area is depleted of flowers for re-seeding, as there are always many flowers yet in bud left. The method should have relatively little effect on the structure of the population.

TABLE 1

VARIATION IN PETAL NUMBER IN THE FLOWERS OF SANGUINARIA CANADENSIS. SUMMARY FOR SIX YEARS OF COLLECTING

Petal No.	3	4	5	6	7	8	9	10	11	12	13	14	15	21	Total
Year															
1926		2	1	8	16	835	24	15	18	26	7	10	2		964
1932		0	2	10	61	1,816	269	105	64	40	1	1	2		2,371
1934		2	5	25	165	4,965	785	493	296	212	34	10	2		6,994
1938		0	3	28	127	6,571	564	277	138	73	9	7	4	1	7,802
1940		6	6	28	189	11,315	669	288	182	135	15	5	3		12,841
1942	1	0	4	5	44	6,738	521	292	173	125	13	2	0		7,918
Total ...	1	10	21	104	602	32,240	2,832	1,470	871	611	79	35	13	1	38,890

In Table 1 a summary of all collecting for 6 years and for all areas is given. From this table it will be noted that the modal petal number is 8, with a mean lying between 8 and 9 and closer to 8. Extreme variants range from one flower with 3 petals to one with 21 petals. There are more than 10 times as many 8-petal flowers as the next most numerous class of 9 petals. The curve of variation is definitely skewed toward petal numbers above 8.

The data by years for complete collections from the two populations already mentioned are given in Table 2. From the totals, if we assume that the Overton Road sample, which is the larger, represents the theoretical distribution of variants for the species, a $2 \times n$ table may be constructed for the Little Apple Creek population. Such analysis gives a chi-square which is highly significant. Thus on the basis of the total samples the two populations differ significantly in petal number. Furthermore, following the same procedure for collections for each year the differences are significant except for the 1942 collections, where the differences are of doubtful statistical significance.

TABLE 2

VARIATIONS IN PETAL NUMBER IN TWO POPULATIONS OF SANGUINARIA CANADENSIS

Petal No.	3	4	5	6	7	8	9	10	11	12	13	14	15	21	Total
Overton Road Population															
Year															
1932		0	2	10	61	1,816	269	105	64	40	1	1	2		2,371
1934		0	1	8	46	3,473	648	378	237	172	27	8	2		5,000
1938		0	2	10	72	4,537	394	185	80	40	5	5	1	1	5,332
1940		1	3	15	129	4,337	371	149	84	62	7	2	0		5,160
1942	1	0	0	1	17	2,511	215	90	43	36	1	1	0		2,916
Total ..	1	1	8	44	325	16,674	1,897	907	508	350	41	17	5	1	20,779
Little Apple Creek Population															
Year															
1934		2	4	17	119	1,492	137	115	59	40	7	2	0		1,994
1938		0	1	18	55	2,034	170	92	58	33	4	2	3		2,470
1942		0	4	4	27	4,227	306	202	130	89	12	1	0		5,002
Total ..		2	9	39	201	7,753	613	409	247	162	23	5	3		9,466

From the data in Table 2 combined with field observations, certain tentative conclusions may be drawn. These two populations differ in respect to the distribution of variants in petal number when collections over a period of years are considered. The Little Apple Creek population gives relatively larger numbers of low petal number types and the Overton Road population relatively larger numbers of high petal number types. However, such a conclusion might well be missed by taking collection records for only one year (see 1942). These larger populations are in turn made up of smaller subgroups. It is the usual thing to find flowers with more than 8 petals together in small subpopulations a few feet or yards in diameter. Some of these plants belong to clone cultures, as the rootstocks branch. Also flowers of less than 8 petals tend to occur close together. But there is no tendency

for flowers of more than 8 and flowers of less than 8 petals to be associated. It would seem likely that different genetic factors condition high petal number from those conditioning low petal number. Furthermore, since variants of 9, 10 and 11 petals are often grouped together the exact petal number is probably influenced by modifying factors, genetic and/or environmental. In fact, transplantation of some of the rootstocks and subsequent flowering have indicated that both genetic and environmental modifiers are at work. Some years ago a bloodroot flower with over 60 petals was brought to the laboratory. This came from a plant found in the wild and transplanted to a garden. It was undoubtedly a mutant to a "double" form and distinct from the factors dealt with in our studies.

The collections for 1942 both from Overton Road and Little Apple Creek show one peculiarity in common. In both populations the number of variants below 8 petals is very low when compared with other years. There has been no corresponding drop in the number of variants of more than 8 petals. It seems hardly likely that both of these populations, quite distinct from one another, should suddenly fluctuate in their genetic makeup so markedly and in the same direction in the same year. Rather it would seem more plausible to interpret the results in terms of some combination of factors in the growing season, perhaps temperature and moisture relationships, conditioning a phenotypic suppression of low petal number. However that may be, the case emphasizes the importance of studies based on collections made from more than one growing season in establshing the facts concerning variation between two populations. During the course of these investigations we have noted other morphological changes, particularly difference in petal shape, in which the distribution indicated a genetic basis.

It has not been deemed either necessary or expedient to present any extended statistical analysis of this material. Such analyses imply a finality which the nature of the data almost certainly does not justify. In this case it seems likely that we are dealing with genetic factors which form microgeographic races (Epling and Dobzhansky, 1942). It would be of interest to secure data from the other parts of the geographic range of Sanguinaria for comparison with these local populations. This has been done for sepal number in *Hepatica acutiloba* by Anderson (1936). It is realized that we present here only a small and imperfect frag-

ment of the pattern of variation in one species as it occurs through the years.

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A CYTOLOGICAL STUDY OF THE GENUS SORGHUM: SUBSECTIONS PARA-SORGHUM AND EU-SORGHUM[1]

THE genus *Sorghum* includes species with haploid chromosome numbers of 5, 10 and 20. Snowden (1936) has divided the genus, on a morphological basis, into two subsections: Para-sorghum and Eu-sorghum. All the species reported to date in the subsection Para-sorghum have a haploid chromosome number of five. Excepting *S. halepense* (n = 20), all the species in the subsection Eu-sorghum have a haploid chromosome number of 10. According to Snowden (1936), although no evidence is offered, the species of the subsection Para-sorghum have played no rôle in the evolution of species in this genus with higher chromosome numbers. The data from this preliminary cytological study suggest that the separation of the species into two groups appears to be a valid one. Indeed, there is reason to believe that the separation may be greater than implied by the subsectional status of the two groups.

The following species were grown at the University of Minnesota, St. Paul, and the University of California, Berkeley: *S. dimidiatum, S. versicolor* and *S. purpureo-serecium* (Para-sorghum); and *S. vulgare, S. sudanense, S. halepense* (Eu-sorghum). Panicles were fixed in a glacial acetic acid-alcohol solution (1 : 3). Smear preparations were used throughout with acetocarmine as staining agent.

[1] The main part of the work for this paper was done at the Division of Agronomy and Plant Genetics, University of Minnesota, St. Paul, during a research assistantship (1941–42). The author wishes to express his gratitude to Dr. C. R. Burnham, whose suggestions and criticisms throughout the work were invaluable.

The chromosome complements of the species in the subsection Para-sorghum were morphologically similar in all phases of meiosis. No marked differences were evident so that any one complement would have been indistinguishable from the others. The chromosome complements of the species in the subsection

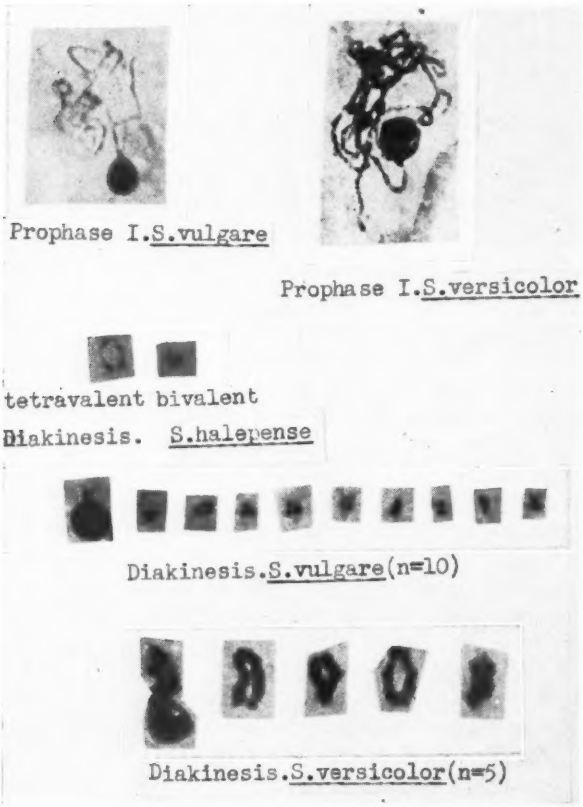

FIG. 1.

Eu-sorghum were likewise morphologically similar in all phases of meiosis and, excepting chromosome number, no marked differences in morphology were evident. However, there were great differences in many characters between chromosome complements of the two subsections.

In the subsection Para-sorghum, the chromosomes at prophase

I stained uniformly throughout with acetocarmine. However, the chromosomes were so long and entangled that it was extremely difficult to determine chromosome lengths with assurance. These chromosomes appeared to be much longer than the familiar chromosomes of *Zea mays* at the same stage. The chromomeric structure was very clear.

The chromosomes of the species in the subsection Eu-sorghum at prophase I did not stain uniformly with acetocarmine. The stain tended to accumulate in the regions adjacent to the centromere. No attempt was made to determine the extent to which the selective staining was restricted to definite lengths of each chromosome arm. The chromosomes at prophase I were much shorter than those of the subsection Para-sorghum. The relative chromosome lengths in *S. vulgare* have been reported by Longley (1937). The chromomeric structure was not very clear, but close examination revealed the presence of chromomeres.

An outstanding morphological difference between chromosome complements of the two subsections was found in the nucleolar chromosome at prophase I. In species of the subsection Para-sorghum, the nucleolar chromosome was terminally attached to the nucleolus. The region of attachment was marked by a heteropycnotic, spheroidal bulge (not a satellite), separated from the remainder of the chromosome by a narrow, non-staining band. In the species of the subsection Eu-sorghum, the nucleolar chromosome was attached to the nucleolus at an intercalary point which did not appear to be morphologically distinguishable from the remainder of the chromosome.

The chromosome complements of the two subsections still displayed striking differences in morphology and size at diakinesis. It was possible to see the internal structure of the chromosomes of the species in the subsection Para-sorghum because of their relatively large size. These chromosomes at diakinesis were 10 to 15 times longer and 2 to 4 times thicker than chromosomes of the species in the subsection Eu-sorghum. It was not possible to see any internal structure in the chromosomes of the latter subsection because of their relatively small size. Again, all the chromosome complements within one subsection appeared strikingly similar at diakinesis.

At no time were multivalents observed in the species of the subsection Para-sorghum. Both *S. vulgare* and *S. sudanense* (Eu-sorghum) appeared to be diploid in that only bivalents were observed. However, univalents, bivalents, trivalents and

tetravalents were found in *S. halepense* (n = 20). No chromosome associations higher than tetravalents could be definitely established in this species.

The chromosome configuration attached to the nucleolus in diakinesis in *S. halepense* was either a bivalent or a tetravalent. The maximum number of tetravalents observed in a single pollen mother cell was five. The numbers of tetravalents per p.m.c. ranged from zero to five. These data are based on 500 p.m.c. obtained from plants originating in Oklahoma and South Carolina. However, there is no reason to conclude that five tetravalents represent the total possible number of tetravalents nor that the same chromosomes are always contributing to the number of tetravalents observed.

The tribe Andropogoneae includes the genus *Sorghum* and allied genera. It was considered probable that there were species in the tribe Andropogoneae which have a chromosome complement not a multiple of ten but of five. No such chromosome number had been reported in the literature. Of the species examined, *Hyparrhenia hirta* was found to have a haploid chromosome number of 15. Incidentally, a reciprocal translocation was found in this species.

DISCUSSION

The cytological evidence suggests that the division of the genus *Sorghum* into two subsections by Snowden (1936) on a morphological basis is not only sound but a natural one. If such striking differences in chromosome morphology as are found between species in the two subsections are significant, then the species in the subsection Para-sorghum have indeed played no rôle in the evolution of species in this genus with higher chromosomes (Eu-sorghum). Taxonomically, there appears to be no doubt that these two subsections seem to belong in the one genus. Although the data are still meager, there is reason to believe that the two subsections may merit separation into two genera. No hybridization occurs between species in different subsections (O'Mara, unpub.).

Cytological and preliminary breeding data indicate a very close relationship among the species of the subsection Eu-sorghum. Excepting for chromosome number, *S. halepense* is essentially different from other species in this subsection only in that it is a perennial while the others are annuals. There is no doubt that

this species is a polyploid, but it is not definite from cytological data whether *S. halepense* is an auto- or allopolyploid. Longley (1932) suggests that *S. halepense* is an autotetraploid. Karper and Chisholm (1936) conclude from their data that more than a mere doubling of the chromosome unmber resulted in the production of the polyploid species. This conclusion may find confirmation in that observation that the possible range of tetravalents (0 to 10) was not found in *S. halepense.*

Huskins and Smith (1932) conclude from data on somatic chromosomes that *S. halepense* is an allotetraploid, the product of a chromosome doubling in a hybrid between a species of *Sorghum* with a haploid chromosome number of 10 and a species in the tribe Andropogoneae, presumably with a haploid chromosome number of 10. In a subsequent paper dealing with the meiotic chromosome in the genus *Sorghum,* Huskins and Smith (1934) report tetravalents and hexivalents in *S. vulgare* and hexivalents in *S. halepense.* Considering all the data, they suggest that the basic chromosome number for the genus *Sorghum* may be seven and not ten. However, no multivalents were observed in *S. vulgare* or *S. sudanense* ($n = 10$); no hexivalents were found in *S. halepense* ($n = 20$) but univalents, bivalents, trivalents and tetravalents. It is more probable that the basic chromosome number for the genus *Sorghum* may be five. It appears to be more than coincidence that the subsection Parasorghum has a haploid chromosome number of five, the maximum number of tetravalents observed in *S. halepense* is five, and a species, while not closely related, in the tribe Andropogoneae, *Hyparrhenia hirta,* has a chromosome number ($n = 15$) which is a multiple of five and not ten or seven.

There still remains the problem of the origin of *S. halepense.* Breeding and cytological data indicate a very close relationship with the species of *Sorghum* with a haploid chromosome number of 10. It is very likely that one of these species was involved in the production of *S. halepense.* However, there are no clues concerning the other putative parent involved in the supposed hybrid which gave rise to *S. halepense.* There is no reason to assume that this putative species belongs to a genus other than *Sorghum,* as was suggested by Huskins and Smith (1932).

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THE NEMERTEAN GORGONORHYNCHUS AND THE FLUCTUATIONS OF POPULATIONS[1]

IN a paper (Wheeler, 1942) discussing the significance of the recent discovery of nemerteans with a type of proboscidial apparatus heretofore undescribed, the naive suggestion is made that the branched type of proboscis peculiar to Gorgonorhynchus may have originated within the past forty years from a form with a simple tubular organ. The only grounds for this conclusion were that two species of the new form were found almost simultaneously on the coasts of Australia, India and Bermuda and that they had not been reported by earlier investigators who had made collections in the same regions.

It was considered remarkable that a species now plentiful on the shores of Bermuda was not found either by Verrill or by Coe, who had searched the same localities near the beginning of the present century. Considering also the circumstance that certain other species of nemerteans which were found at Bermuda forty years ago have not been seen recently, Wheeler infers that one of them may have been the "mutation mother-species of Gorgonorhynchus by development from the eggs." What a thrill it would give to students of evolution if such an inference could be substantiated. But since that seems to the writer unlikely of realization, a simpler explanation and one more in harmony with the behavior of littoral populations may be appropriate.

There is, of course, a possibility that the species has but recently arrived at Bermuda on the bottoms of ships, as suggested by Zimmerman (1943) and also considered by Wheeler, but such a distribution of a burrowing worm with the habits of Gorgono-

[1] Contributions from the Scripps Institution of Oceanography of the University of California, La Jolla, New Series, No. 218.

rhynchus seems improbable. More seriously to be considered is the factor of chance. The combined intertidal shorelines of all the Bermuda islands extend for more than fifty miles, along which are innumerable stones that would form suitable protection for the nemertean. It is safe to say that relatively few of these stones have even yet been lifted to expose the treasures which may lie beneath them. Perhaps it was only by a mischance that neither Verrill nor Coe happened to look under just those stones which concealed a worm with such an aberrant structural modification that neither could have failed to notice if such a worm had been seen. The writer is unwilling to admit that human eyes are any sharper to-day than they were at the beginning of the century.

It is obvious that the chance of finding a representative of a species will increase rapidly as the number of individuals in the population becomes greater. And it would be unusual if any population remained constant in numbers. Every observer of long experience has witnessed many such fluctuations in abundance from year to year.

Populations wax and wane; periods of abundance are followed by others of relative scarcity or complete disappearance (Clements and Shelford, 1939; Coe and Allen, 1937). Such periodicities are as characteristic of the populations of littoral worms as of other organisms. They are so familiar to all biologists that it seems unnecessary to mention specific examples.

New species of animals and plants are being discovered in familiar localities every year; numerous individuals of the new type may appear suddenly and later disappear with equal rapidity. Dominant populations may be replaced by others, quickly or over a period of years. An increase in one locality may accompany the decrease or the complete disappearance of the same species in certain other regions.

Some of the described species have as yet been reported on but a single occasion. Their discovery may have been due to the circumstance that one or more individuals wandered from the usual habitat of the species. As the population increases a wider dispersal is likely to ensue. As an extreme example may be mentioned a species of nemertean of which two individuals, each more than a foot in length, were found on the shore at Woods Hole, Mass., during an extremely low tide in June, 1894. Their morphological peculiarities were such as to make them the type

of a new genus (Parapolia). In spite of persistent search in the same locality and elsewhere during many of the intervening years, no additional representatives of the species have been found. And yet it seems not improbable that numerous individuals are living somewhere in the vicinity, perhaps somewhat below the low-water mark, for in such situations burrowing animals are difficult to obtain.

It may be assumed therefore that "Polia or Eupolia," which is mentioned by Wheeler as the possible "mutation mother-species" of the form with branched proboscis, is not "moribund" and it may be confidently expected that it will appear again in full vigor and quite unchanged by the allegation that it is at present masquerading in the guise of Gorgonorhynchus.

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